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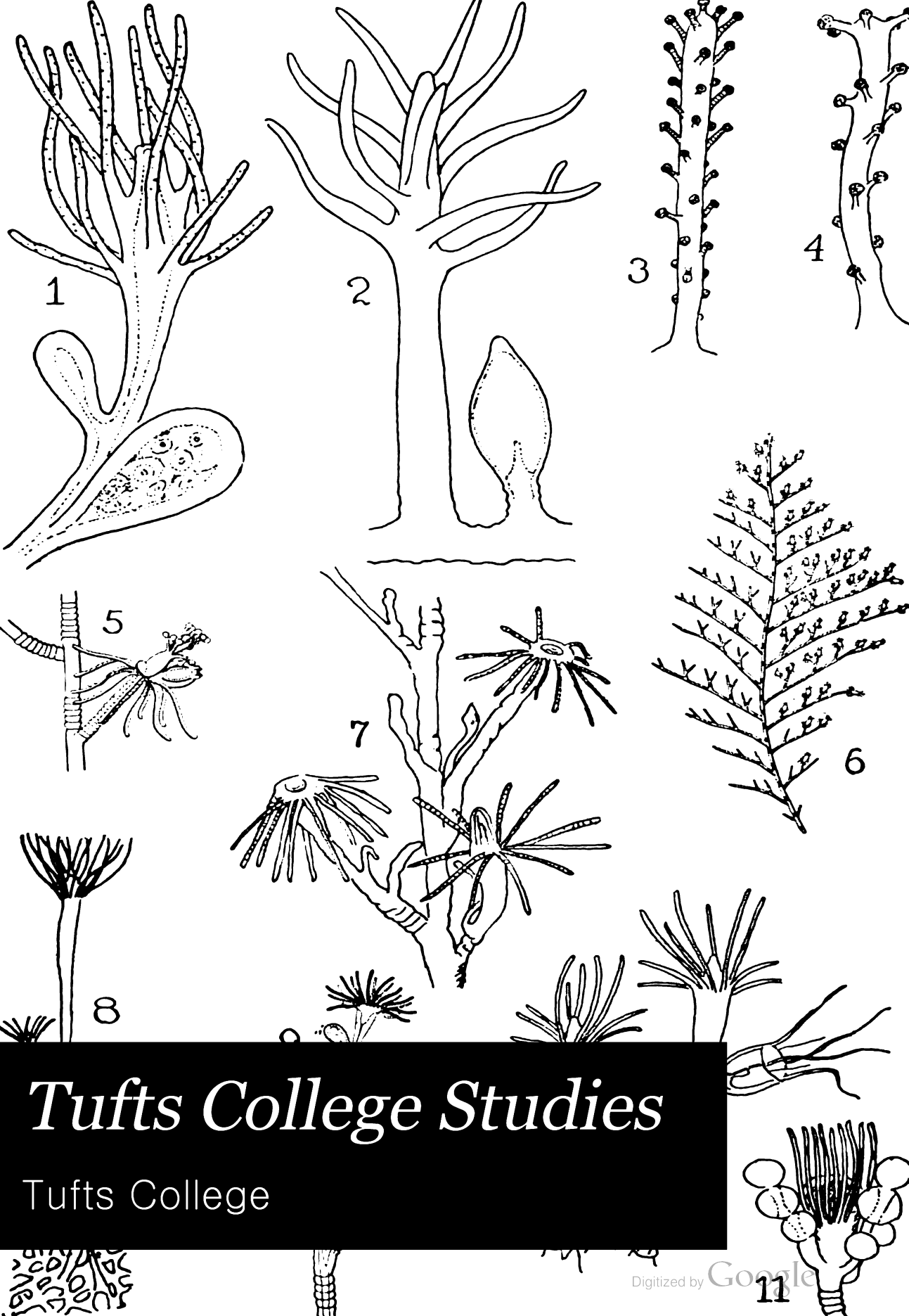

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TUFTS COLLEGE STUDIES, Vol. III, No. 1.

(Scientific Series.)

TWO NEW SPECIES OF CHARACIUM. By F. D. Lambert.

A SYNOPSIS OF THE FIXED HYDROIDS OF NEW ENGLAND. By J. S. Kingsley.

WET AND DRY DIFFERENTIATION OF IGNEOUS ROCKS. By A. C. Lane.

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TUFTS COLLEGE, MASS.
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TUFTS COLLEGE STUDIES, Vol. III, No. 1.

TWO NEW SPECIES OF CHARACIUM.*

By F. D. Lambert.

(Plate 1.)

Characium gracilipes n. sp. Cellula 80–480 μ longa, 5–13 μ diam., regulariter curvata, parte media fusiformis, superne in setam longam, inferne in stipitem longam filiformem attenuata, rhizoideis minutissimis substrato affixa.

Cells 80–480 μ long, 5–13 μ diameter, regularly curved; middle part fusiform, tapering above into a long hair, below into a long filiform stipe, attached to the substratum by very minute rhizoids.—On the minute crustacean, *Branchipus vernalis*, Medford, Massachusetts, May, 1903, 1904, 1905, and 1906.

In May, 1903, while I was collecting with a class in biology, in Medford, Mass., on the edge of the Middlesex Fells, one of my students called attention to a small green object moving about in a small pool. On examination it proved to be a fairy shrimp, *Branchipus vernalis*, one of the animal forms for which I was searching, and as its color was so very unusual, a number of the animals were collected and carried to the laboratory. A microscopic examination showed that the green color was due to masses of green algae attached to various parts of the body, particularly to the appendages. As it seemed likely that the plant might be of interest and perhaps also might be desirable for distribution in the Phycotheca Boreali-Americana, some of the Branchipus were submitted to Mr. F. S. Collins for identification of the algae. He immediately reported that they were apparently two new species of Characium. Only a few of the Branchipus were collected that spring; in the spring of 1904 a few more were collected from the same pond; but not until the

* Contributions from the Biological Laboratories of Tufts College, No. 48. Reprinted from *Rhodora*, vol. 11, pp. 65–74, Plate 79, April 1909.

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spring of 1905, however, were conditions favorable for collecting the material in sufficient quantity for the P. B.-A. sets. At that time there was but little water in the pool, and it lowered so rapidly during the time Branchipus were present, that the animal was driven gradually toward deeper water. I was able to scoop up with a net from the muddy hole in the middle of the pool, about a pint of specimens, which I preserved in 5% formaldehyde. Other pools in the vicinity were frequently but unsuccessfully examined. Only the one pool contained it, and in such abundance that a recent examination of the material collected in 1905 showed the Characia attached not only to Branchipus, but also to mosquito larvae, which had been overlooked at the time of collection. In May, 1906, a few sketches, not more than eight or ten, were made from a small number of specimens collected at that time, but the scarcity of Branchipus made it advisable to postpone further investigations until the next spring, when, it was hoped, material would be sufficiently abundant for a study of the reproduction. Failure to find the material in 1907 and in 1908 leads me to fear that it may have disappeared entirely; hence the publication of the present account founded almost wholly on material which was collected in 1905 and preserved in formalin, and from which sets for the P. B.-A. were prepared.*

Characium gracilipes occurs in greatest abundance on the flat surfaces of the two sides of the abdominal appendages of Branchipus, and rarely on the marginal hairs for which *Characium cylindricum* seems to show a preference. Both species, however, may be found on the head, antennae, and mouth-parts, and dorsal surface of body and tail. In respect to size, both *Characium gracilipes* and *Characium cylindricum* differ greatly from all species heretofore described: the smallest specimen of *Characium gracilipes* which I measured, 80 μ, was almost as long as the extreme length given by West † for *Characium ensiforme* Herm,

* In order to prepare the material for the P. B.-A., about 500 formalin specimens of Branchipus were spread out to dry on a clean sheet of glass. When dry, they were fastened on mica with glue, two or three specimens on a piece. *Characium gracilipes* P. B.-A., No. 1270; *Characium cylindricum* P. B.-A. No. 1269.

† West, G. S. The British Freshwater Algae, Cambridge, 1904, p. 200.

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86 μ, which, he states, "is the most elongate species of the genus." The longest specimen of *Characium gracilipes* which I observed, measured 480 μ, nearly six times as long as the maximum length for *Characium ensiforme* Herm.

The stipe and terminal hair are in line with the general curve of the body (fig. 4, pl. 1). The one cell stage of *Characium gracilipes* reminds one of *Closterium rostratum* Ehrenb., as figured by West.* In later stages during spore formation a more pronounced curvature frequently accompanies the elongation of the body, but it seldom exceeds an angle of 90°, and is always simple and in one direction.

The terminal hair, open throughout its entire length but closed at its distal end, is about the same length in all specimens, and always shows a sharp demarcation from the fusiform body, from the apex of which it emerges. The lower end of the fusiform body tapers gradually into the stipe, also like the terminal hair, of capillary dimensions and hollow. The stipe is closed at a point very near its base. The base of this plant is remarkable in that it adds a new character for Characium, viz., the presence of minute rhizoids. These are of different forms, but the most typical is that shown in figures 3, 4, 5, 6 and 9 (pl. 1), which show two smooth, straight, slender, solid processes emerging from the closed base of the stipe, with which and with each other, the rhizoids form three approximately equal angles of about 120° respectively. This divergence is almost always evident, inasmuch as the rhizoids are in the same plane as the line of curvature, and as the specimens can naturally take but one position in the narrow space between the slide and cover. These processes, usually of the same length vary from 2 to 10 μ. Fig. 22 (pl. 1) illustrates the largest observed.

Pl. 1, fig. 14, shows two rhizoids of approximately equal length, emerging at the same angle on one side of the stipe; fig. 15, rhizoid of one side with a hook turning inward; fig. 17, two rhizoids with hooks turning outward; fig. 16, two rhizoids depending from base, like a two-tined pitch-fork, not an uncom-

* West, G. S. A monograph of the British Desmidiaceae. Vol. I, Pl. XXVI, fig. 1.

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mon condition; fig. 20, two rhizoids of the normal shape, but of unequal length; fig. 19, three rhizoids, a very rare condition; figs. 18 and 21, rhizoids of normal type with a tendency toward a branching which may vary from merely slight roughenings and thickenings to well-defined short branches. This condition is more common than that of fig. 19, but occurs less frequently than others. For a long time I really doubted this form, thinking the branched appearance might be due to the presence of detritus not unusual about the bases of the rhizoids. As efforts to dislodge these branch-like processes from the rhizoids failed, I concluded that in some cases, at least, the branching was real. The rhizoids penetrate the mucus on the surface of the appendages, and are well adapted to retain a hold on the swimming Branchipus. At first glance the rhizoids, particularly the short ones, might easily give the impression that the base consists of a disc seen in optical section, but careful observation with ordinary high powers, as well as with oil-immersion lens, proves the fallacy of this supposition. This suggests a possibility that some of the structures, hitherto described in other species as discs, may have been, in some instances, rhizoids which, on account of insufficient magnification, have escaped detection.

The single parietal chromatophore shows a single conspicuous pyrenoid on the convex side of the cell, a position which the pyrenoids continue to occupy in the later stages during the entire process of transverse segmentation of the protoplast. The pyrenoid appears as a highly refractile body, spherical or ovoid in outline, separated from the chlorophyll-bearing part of the chromatophore by a narrow hyaline zone; always visible, it can be followed very easily in all the phases of its division and movement during the process of spore production. See figs. 3, 4, 5, 6 and 9 (pl. 1). The division of the pyrenoid is accompanied by a simultaneous division of the chromatophore into two equal parts. The pyrenoid, in dividing, first elongates, then, by a median constriction, assumes a dumb-bell shape, and finally divides into two parts, each of which assumes the original rounded form. The division of the pyrenoid is the first visible evidence of spore development.

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The usual method of spore formation is by repeated transverse division of the protoplast, which gives 32 cells arranged in a single series. Next, by longitudinal division, each of the 30 cells in the middle of the plant divides into two cells; at the same time, the basal and the terminal cells divide transversely, thus giving 64 cells, the maximum observed. See figs. 6 and 9 (pl. 1), the latter representing the basal (z) and terminal (x) portions of a plant containing 64 spores. The general plane of longitudinal division throughout the mother cell is usually continuous. Although this is the usual method of division, occasionally the longitudinal division occurs in an earlier stage. Fig. 5 (pl. 1) shows the longitudinal division appearing in the 4 cell stage. In other instances the longitudinal division first occurred in the 8 and in the 16 cell stage of the uniseriate type. The division of basal and terminal cells is always transverse, never longitudinal. At any stage, a count of cells and a careful examination of the pyrenoids leads to the conclusion that the divisions are approximately simultaneous throughout the length of the cell; the evidence, while not conclusive, suggests that a cell, once divided longitudinally, does not divide again in any plane. Elongation of the individual is not always correlated with the progress of spore formation. Some individuals in incipient 2 or 4 cell stages are as long as others in fully developed 8 cell stages. Among the thousands of specimens that have been under observation, I have been unable to find any trace of the liberation of the spores, or of their germination; any empty cells; or any evidence of the spores assuming the rounded form characteristic of *Characium cylindricum* and of other species which have been hitherto described. A microscopic examination of Branchipus bearing the Characia always shows many specimens of *Characium gracilipes* broken, especially in the advanced stages of spore formation. These broken cells, however, present no evidence of the escape of the contents, save at the very ends, and there, only a few cells. There is no uniformity in the length of the broken pieces, nor in their stage of development. They may vary from early stages up to the 64 cell stage. Basal, middle, and distal portions appear in the field at once, which leads one to think that the elongated *Characium*

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gracilipes had been broken up mechanically in the manipulation of the material under the cover-glass. An examination of entire specimens of Branchipus, under conditions where the chances of mechanical disturbances were at a minimum, still showed broken specimens. Moreover, inasmuch as the formalin had not caused any appreciable swelling, this broken condition could not be ascribed to the effect of the preservative. If fragmentation be the normal method of spore liberation, it is difficult to understand what becomes of the empty cells, and why there is no satisfactory evidence of liberation of the spores. If this fragmentation of *Characium gracilipes* be characteristic for the species, it may be that the liberated cells, on dissolution of the containing wall, assume the palmelloid state which has been described for other species. I have not seen eivdence of the palmelloid condition. It seems strange that none of the germinating spores could be found; the smallest specimen observed measured 80 μ in length, and was fully developed in every respect.

Characium cylindricum n. sp. Cellula 24–430 μ longa, 10–20 μ diam., cylindrica, apice rotundata, basi in stipitem brevem attenuata; disco basali nullo.

Cell 24–430 μ long, 10–20 μ diam., cylindrical, with rounded apex, base tapering into a short stipe, without basal disc.—On the minute crustacean, *Branchipus vernalis*, Medford, Massachusetts, May, 1903, 1904, 1905 and 1906.

Characium cylindricum, in the one cell stage (figs. 10, 11, 12 and 13, pl. 1), has a central nucleus and two parietal chromatophores. The chromatophores almost completely line the circumference of the cell, are slightly but distinctly separated from each other, thus affording a good view of the nucleus, situated near the middle of the cell, and are without pyrenoids. Numerous small oil globules are often present in the cell. The lower portion of the cell tapers into a very short stipe with base rounded or pointed and often slightly bent at the place of attachment to the substratum.

Characium cylindricum occurs in greatest numbers upon the marginal hairs (on both main shaft and small branches) of the appendages of *Branchipus vernalis*, but may occur anywhere on the appendages.

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Each individual is attached by means of a small, brownish, mucilaginous mass, distinct in outline, and usually very conspicuous on account of the detritus present upon its surface. See fig. 25 (pl. 1). The transparency of the chitinous wall of the hair affords an excellent opportunity to study the attachment from any point of view. In fig. 25 (pl. 1) the cell (a) is attached to the under side of the hair. The adhesive substance, when circular in outline, might easily be mistaken for a disc, did not its transparency permit a clear view of the pointed or rounded outline of the wall at the base of the cell. Whenever the cell is attached to two or more of the smaller hairs, they incline toward a common point of crossing, at which point the mucilaginous substance adheres. This method of attachment seems quite as well adapted to its function as do the rhizoids of *Characium gracilipes*. When *Characium cylindricum* cells become detached from the hairs by mechanical disturbance of the cover glass, the adhesive substance usually sticks to the substratum, and the basal ends of the cells are clean, as illustrated in figs. 1, 2, 7, 8, 10, 11, 12, 13 and 24 (pl. 1). Observations under conditions of minimum mechanical disturbance show small patches of the adhesive substance here and there on the hairs, thus indicating that the cells of *Characium cylindricum* occasionally become detached from the live Branchipus.

By repeated transverse divisions the protoplast of the single cell divides into 8, 16 or 32 spores, fig. 24 (pl. 1). The regularity of approximately transverse divisions is frequently varied by a tendency toward the oblique, which may be confined to a few cells only, or may extend to the entire series. Longitudinal division usually begins after the protoplast has divided into 8 or 16 cells, though it may occur as early as the 4 cell stage. However, the above mentioned obliquity of the transverse divisions is usually so marked in the later stages (8–16 cell) that it is extremely difficult to determine whether division is transverse or longitudinal. In the individual illustrated in fig. 1 (pl. 1) there are eight spores, apparently motile, a condition still further confirmed not only by their arrangement and shape, but also by the presence of the hyaline papilla (p) at the anterior end, in connection with which I observed evidence of flagellae

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too indistinct to be studied. One of the spores (b) is seen escaping from a lateral aperture. There were but eight spores in the specimen shown in fig. 1 (pl. 1), but the unoccupied space in the containing cell would seem to indicate that the original number might have been 16, eight of which had been liberated. Fig. 7 (pl. 1) illustrates a cell containing 32 spores, which, from all appearances, were motile at the time of fixation. As the small amount of unoccupied space in the cell precludes 64 as the original number of the spores, it seems safe to assume that none of the spores had escaped. Apparently not more than eight or ten of the spores had been actively motile up to the time of fixation; moreover, with exception of the two detached spores near the base, the spores in the lower two-thirds of the cell present the usual appearance of the protoplast after its division into 32 cells. The difficulty, previously mentioned, of interpreting the direction of planes of division is well illustrated in this specimen.

In another type of spore formation, by a process of segmentation, in its early stages indistinguishable from the foregoing, the protoplast divides into a very large number of small spores (fig. 8, pl. 1). In the more elongated specimens the number of these small spores certainly exceeds 1000, and in some cases perhaps 2000. Their number is not constant, however, as advancement in segmentation is not co-ordained with the length of the specimen. Moreover, it is certain that these small spores, when fully developed and ready to escape from the cell, are not of uniform size. The few scattered spores near the base of the cell, the perforated apex of which appears in fig. 23 (pl. 1), measured 3 μ, certainly much larger than those which appear in fig. 8 (pl. 1). In the formalin material it was impossible to distinguish any details with respect to the flagellae of these spores, or to determine what becomes of any of the motile cells. Perhaps they are the micro- and macro-zoospores mentioned by Oltmanns,* as described by Reinhardt.†

* Oltmanns, Dr. Fr., Morphologie und Biologie der Algen, Jena, 1904, Bd. 1, p. 175, quoting.

† Reinhardt, L., Entwickelungsgeschichte der Characien. Protok. d. Sekt.-Sitz., d. 5. Vers. Russ. Naturf. u. Arzte in Warschau, 1876. Jahresber. 4, p. 50.

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Although *Characium cylindricum* is characterized by so many features, visible nucleus, two cromatophores, oil globules, absence of pyrenoids, peculiarity of attachment, and peculiarities of reproduction, at variance with what have been accepted up to this time as generic characters of Characium, it does not seem advisable to make a new genus for this form, without further study of living material.

Reinsch* has described a minute alga, *Dactylococcus Hookeri*, which he found growing attached to the small crustacean, *Cyclops bicaudatus*, collected in the neighborhood of Erlangen, Germany, in 1872. In 1874 he found another form, *Dactylococcus De Baryanus*,* growing on the same crustacean, *Cyclops bicaudatus*, collected in the same region. In the summer of 1877 he found the latter form, *Dactylococcus De Baryanus*, on "a somewhat smaller species" of *Cyclops* from pools a few miles west of the southern end of Lake Michigan. Again in the following summer, 1878, he discovered *Dactylococcus De Baryanus*, on *Cyclops bicaudatus* and on a species of *Lepidurus*,† taken from the water mains of the city of Boston. As Mr. F. S. Collins regards both of these species of Dactylococcus as belonging to the genus Characium, it is of interest to note what Reinsch ‡ has described for the reproduction of *Dactylococcus De Baryanus*, the species which he found here in the vicinity of Boston. He describes as the earliest stage of development a slow-moving, green amoeboid cell of about 25 μ diameter, with red stigma. When these cells are elongated they have at the anterior hyaline end a single vibratile flagellum terminated by a bead-like thickening. After a short time these cells lose their power of movement, attach themselves to the surface of the crustacean, and quickly develop

* Reinsch, P. F., Contributiones ad Algologeam et Fungologeam, p. 78, pl. 11.

† In referring to the crustaceans found in the water mains of the city of Boston, Reinsch says, "Am 20 Juni waren die meisten untersuchten Thierchen (*Cyclops bicaudatus* und einer *Lepidurus*-species, von der deutschen verschieden) mit Parasiten besetzi." Inasmuch as Lepidurus is not known to occur east of the Great Plains, it is impossible to say what crustacean is referred to here.

‡ Reinsch, P. F., Beobachtungen über entophyte und entozoische Pflanzen parasiten. Botanische Zeitung, 1879, p. 38, pl. 1, figs. 21–24.

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into the adult Dactylococcus, the protoplast of which finally becomes divided into three or more daughter cells. The subsequent history of these daughter cells was not observed. Whether these features which have been described for *Dactylococcus De Baryanus* offer any solution for the gaps which at present I am unable to bridge in the life history of *Characium gracilipes* and *Characium cylindricum*, cannot be told until further observations can be made on living material of the two species of Characium and, if possible, on *Dactylococcus De Baryanus* itself.

Characium gracilipes and *Characium cylindricum* are hosts of a fungus, two stages of which are figured. Fig. 3 (pl. 1) shows an early stage; a late stage is represented in fig. 2 (pl. 1). The fungi occur attached to any part of either species, except the rhizoids and the distal region of the terminal hair in *Characium gracilipes*, and the region of attachment in *Characium cylindricum*. Presence of the fungus usually produces considerable modification in the shape of the Characium. In the earlier stages of the development of the fungus, the protoplast of the host shows a slight disturbance which increases as the development of the fungus advances. By the time the fungus has reached maturity, the protoplast of the host has usually quite disappeared, fig. 2 (pl. 1). This fungus will be the subject of a later paper.

EXPLANATION OF PLATE.

All figures × 600.

Fig. 1. *Characium cylindricum*, cell containing 8 spores; e, spore escaping from lateral aperture; n, nucleus of spore; p, hyaline papilla at anterior end of spore.

Fig. 2. *Characium cylindricum*, empty cell with mature fungus sporangium (s) attached near distal end.

Fig. 3. *Characium gracilipes*, unicellular stage, with fungus cell (f) attached on side opposite the pyrenoid.

Fig. 4. *Characium gracilipes*, unicellular stage, a typical specimen; py, pyrenoid on convex side of cell; r, rhizoids.

Fig. 5. *Characium gracilipes*, 8 cells, distal and basal cells divided transversely; middle cells divided longitudinally.

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Fig. 6. *Characium gracilipes*, 16 cells dividing to 32 cells by transverse division; all pyrenoids on convex side of cells; a typical condition.

Fig. 7. *Characium cylindricum*, cell containing 32 spores which are apparently motile.

Fig. 8. *Characium cylindricum*, cell developed into sporangium containing many small spores.

Fig. 9. *Characium gracilipes*, distal (x) and basal (z) ends of cell containing 64 spores; distal and basal cells divided transversely; other cells divided longitudinally.

Figs. 10, 11, 12 and 13. *Characium cylindricum*, unicellular stage; n, nucleus; ol, oil globules; two parietal chromatophores.

Fig. 14. *Characium gracilipes*, base of stipe, 2 rhizoids on one side.

Fig. 15. *Characium gracilipes*, base of stipe, two rhizoids, one of which is hooked.

Fig. 16. *Characium gracilipes*, base of stipe, two rhizoids dependent like pitch-fork.

Fig. 17. *Characium gracilipes*, base of stipe, 2 rhizoids, both hooked.

Fig. 18. *Characium gracilipes*, 2 rhizoids with numerous short branches.

Fig. 19. *Characium gracilipes*, 3 rhizoids, an unusual type.

Fig. 20. *Characium gracilipes*, 2 rhizoids, one shorter than the other.

Fig. 21. *Characium gracilipes*, 2 rhizoids with slight roughenings.

Fig. 22. *Characium gracilipes*, 2 rhizoids, the longest observed.

Fig. 23. *Characium cylindricum*, perforated distal end of cell containing spores; h, aperture.

Fig. 24. *Characium cylindricum*, cell containing 8 protoplasts, a typical specimen; n, nucleus.

Fig. 25. *Characium cylindricum*, a, base of cell attached to under side of main shaft of hair; c, base of cell attached to upper surface of main shaft of hair; b, base of cell attached to three of the smaller hairs.

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A SYNOPSIS OF THE FIXED HYDROIDS OF NEW ENGLAND.

By J. S. Kingsley.

Several valuable synopses of the Hydrozoa of New England have been published, some by Professor C. W. Hargitt, others by Professor C. C. Nutting, and thus, to some extent, the present article duplicates their work. They, however, dealt mostly with the forms occurring on the south side of Cape Cod, and consequently several forms from the north of that barrier were omitted, while recent studies, chiefly by Professor Hargitt, have added several species to the list. The present article has aimed to incorporate all of this material and also to arrange it in the form of a key. It may be said that the basis of the paper was written for personal use over twenty years ago, though its last revision dates from the year 1910. Many figures have been copied for the purpose of illustration, but some of the oft figured species are not represented on the plates.

The present paper includes only the fixed or hydroid conditions of the group of Hydrozoa, the medusæ being reserved for a second article, the manuscript for which is nearly complete. In anticipation of the second part there is given here a general account of the whole group of Hydrozoa, in which the various technical terms employed are defined.

The Hydrozoa form one of the two (or three) great divisions or classes of the phylum Cœlenterata. Like the others of the phylum they have the body composed of two cell layers, an outer ectoderm, an inner entoderm, with a third layer, the mesoglœa — sometimes structureless, sometimes containing immigrant cells — between the other two. There is but a single opening from the outside to the interior cavity, and while this is usually called the mouth, it has to serve for vent as well. There is but a single cavity — the gastrovascular space or cœlenteron — which extends from the mouth through all of the ramifications of the body, being sometimes simple, sometimes

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extremely complex, either through branching or by the foldings of the entodermal lining.

The Hydrozoa are marked off from other members of the phylum by some characters, not readily made out in a superficial examination, but of great morphological significance. In all the species the ectoderm and entoderm meet at the mouth, while in the other classes an ectodermal œsophagus of varying extent intervenes between the mouth and the entodermal portion of the gastrovascular cavity. The lining of the digestive cavity may be smooth or thrown into folds (tæniolæ), but gastric filaments protruding from the walls into the cœlenteron never occur. A third feature is that the reproductive cells — eggs and spermatozoa — usually arise in the ectoderm and migrate thence into the mesoglœa. Other features of secondary importance are more easily made out, and these serve for the ready recognition of the members of the group. They are included in the following paragraphs.

In what may be called the typical hydrozoan there is an alternation of generations in the life history, and this results in two greatly different stages, which must be taken into account. One of these is the **fixed** or **polyp** stage, which reproduces asexually; the other is the free-swimming or **medusa** (jelly fish) stage, which produces the eggs and spermatozoa. As will appear, there is an almost infinite series of gradations between these two typical conditions.

In the polyp stage the animals usually reproduce by budding, but as these buds may fail to separate, colonies, sometimes of great extent, result. Each colony consists of enlarged portions or **hydranths**, each with a mouth at the free end of a short proboscis or **manubrium**. Arranged in various ways around the hydranths are the tentacles, each bearing numerous batteries of **nettle cells** (**cnidæ**), which are used in paralyzing the prey. The hydranths are supported on a slender stem, the **hydrocaulus**, which serves to connect all parts of the colony. Frequently a portion of the stem, now known as the **hydrorhiza**, runs in a root-like manner over the object — seaweed, stone, or pile — to which the colony is attached. Branches of the gastrovascular space run through the hydrocaulus and hydrorhiza, so that

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nourishment from each hydranth can be conveyed to all parts of the colony.

At certain places — which may be on hydranth, hydrocaulus or hydrorhiza, according to the species — buds of a peculiar character, the **medusa buds,** arise. These may be isolated, or they may be aggregated in clusters, the **gonophores.** In the typical cases, these medusa buds gradually take the characters of the medusæ and at last separate from the parent and swim away as free jelly fish, to be described below. In other hydroids the medusa buds may remain more or less imperfect and retain their connection with the parent during their whole existence.

In many of the polyps the external surface of the animal has the power of secreting a horny envelope, the **perisarc,** which is protective in character. In many the perisarc is confined to the hydrocaulus and hydrorhiza and is frequently more or less annulate, as if to permit more flexibility in the stems. In other hydroids the perisarc may include all parts of the colony, forming cups (**hydrothecæ**) around the hydranths and capsules (**gonothecæ**) around the gonophores.

At first sight the medusa differs greatly from the hydranth, but more intimate study permits a comparison of part with part in the two. The medusa consists of a circular portion, the **bell** or **umbrella,** from the concave side of which a proboscis or **manubrium** projects like the handle of the umbrella or the tongue of the bell. The mouth is at the tip of the manubrium, while its stalk is occupied by the stomach, which extends up into the centre of the bell. Usually four **radial canals** extend from the deeper end of the stomach, like the ribs of an umbrella, through the substance of the bell to its margin, where they connect with a **ring canal** which follows the margin of the umbrella.

The margin of the bell supports a varying number of tentacles, four of which are placed opposite the ends of the four radial canals, the others, when present, being intercalated between the primary four. (In *Hybocodon* but one tentacle is developed, the others being aborted.)

The umbrellar margin also supports the sense organs when these are present. These may consist of **eye spots** and of

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statocysts. The eye spots are pigmented and are usually on the bases of the tentacles. The statocysts — frequently called ears — are of two kinds. In the one they are open pits or closed vesicles, varying from eight to hundreds in number, placed in the intervals between the primary tentacles. Each contains one or more concrements, the so-called otoliths or statoliths. The other type, which also occurs between the principal tentacles, includes short, modified, club-like tentacles with otoliths in their interior.

A feature which serves to distinguish the hydrozoan medusa from all other jelly fishes is the **velum.** This is a fold of ectoderm just inside the opening of the bell, with an aperture in the centre through which water can enter, and through which, in many species, the proboscis may protrude. In the medusæ of the genus *Obelia* the velum is so reduced as to be hardly recognizable, an exception to the rule of its universal prominence.

The medusæ are the sexual individuals of the alternating generations, and in them the sexes are separate. The reproductive organs (**gonads**) are always developed on the subumbrellar side, sometimes on the lines of the radial canals, sometimes in the wall of the manubrium, the position being of considerable systematic importance.

In the Hydrozoa every conceivable modification of these two alternating extremes — polyp and medusa — may be found. In some (Narcomedusæ, Trachomedusæ, Siphonophores) the polyp stage may be entirely suppressed and the species may reproduce only in the sexual manner; or, in rare instances, medusæ may bud medusæ. On the other hand there may be every step in the disappearance of the medusa stage. In some the medusa is perfectly formed, but it never separates from the parent; setting free the eggs or sperm while attached to the hydroid. In a farther degeneration the mouth of the medusa bud may not open; and from this we way trace a descending scale with gradual loss of tentacles, umbrella, etc., until, as in *Clava*, we have but a rudimentary manubrium with its gonads to represent the medusa. It would appear possible that the bunches of eggs or sperm in *Hydra* are not to be regarded as

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showing a primitive condition, but as the last term of a degenerating series.

In the following analytical keys the polyp stage is alone considered and there is no attempt to connect polyp and medusa. The distribution has been roughly indicated by the letters N and S, indicating the occurrence of the species north and south of the well-recognized barrier of Cape Cod. In many cases there are also brief notes upon the bathymetrical range.

KEY TO THE NEW ENGLAND SPECIES OF FIXED HYDROZOA.

1. Polyps solitary, never colonial; no medusæ or medusa buds; sex cells produced in wall (ectoderm) of polyp. HYDRARIÆ 40
1. Solitary or colonial; perisarc absent or only covering the stems, never expanding into hydrothecæ; reproductive buds never included in gonothecæ. Medusæ with eyes situated usually at the base of the tentacles; gonads on the proboscis of the medusa. TUBULARIÆ (GYMNOBLASTA) 2
1. Perisarc always present and developing hydrothecæ and gonothecæ. Medusæ with vesicular statocysts on the margin of the bell, usually between the tentacles. CAMPANULARIÆ (CALYPTOBLASTA) 42

TUBULARIÆ.

2. Hydranths with scattered tentacles. 3
2. Hydranths with a single whorl of tentacles. 4
2. Hydranths with two or more whorls of tentacles. 7
3. Tentacles simple, filiform; polyps never forming free medusæ. CLAVIDÆ 10
3. Tentacles enlarged at free ends (capitate), some-

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what spirally arranged. Medusæ sometimes becoming free. CORYNIDÆ 15

4. Proboscis conical, not sharply differentiated from rest of hydranth. 5

4. Proboscis trumpet-shaped or hemispherical; polyps never forming free medusæ; male gonophores just beneath the tentacles, female on the body of the hydranth. EUDENDRIIDÆ 19

5. Colony not branched; hydrorhiza forming an encrusting base; colony polymorphic, with two or three different kinds of polyps. 6

5. Colony regularly branched, with distinct perisarc; free medusæ arising from the hydrocaulus. BOUGAINVILLEIDÆ 21

6. Gonophores sessile, never separating as medusæ. HYDRACTINIIDÆ 27

6. Gonophores producing free medusæ. PODOCORYNIDÆ 24

7. Tentacles all non capitate. 8

7. Proximal tentacles filiform, distal capitate. PENNARIIDÆ 29

8. Stem with distinct horny perisarc* 9

8. Hydrocaulus with longitudinal canals; no distinct perisarc; producing free medusæ. CORYMORPHIDÆ 32

9. Distal tentacles in two whorls; producing free medusæ. HYBOCODONTIDÆ 34

9. Distal tentacles not in two whorls; gonophores borne on branched peduncles. TUBULARIIDÆ 37

10. CLAVIDÆ. Unbranched; no perisarc except a very small amount at base. 11

10. CLAVIDÆ. Branched; stems with distinct perisarc. *Cordylophora* Allman 12

11. Gonophores arising from hydranths below tentacles. *Clava* Gmelin 13

*In the single specimen of *Ectopleura prolifica* described by Hargitt no perisarc was found; there is a distinct one in other members of the genus.

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11. Gonophores arising from hydrorhiza.
Rhizogeton Agassiz 14

12. *Cordylophora*. Perisarc frequently annulate, gonophores borne on branches; hydranths with 15-20 tentacles.
C. *lacustris* Allman. fig. 1. S. Fresh and brackish water.

13. *Clava*. Tentacles 20 + in large specimens; salmon or red; on rockweed, etc., between tides.
C. leptostyla Ag. N. S.

14. *Rhizogeton*. Red; about 12 tentacles; hydranths 6mm. high; gonophores oval.
R. fusiformis Ag. fig. 2. N. S. Tide pools.

15. CORYNIDÆ. Stem with horny perisarc; hydranth shorter than stem. *Syncoryne* Ehrenberg 16

15. CORYNIDÆ. Hydrocaulus with horny perisarc; tentacles verticillate, branched, the branches knobbed; gonosome unknown. *Cladocoryne* Rotch 17

15. CORYNIDÆ. No perisarc; hydranths sessile, with long cylindrical bodies. *Corynitis* McCrady 18

16. *Syncoryne*. Irregularly branching; perisarc not annulated; 16 tentacles; medusæ borne on hydranths. *S. mirabilis* (Ag.) fig. 83. On rocks, floating wood, etc. N. S.

16. *Syncoryne*. Sparingly branched; 15-30 tentacles variously arranged on proximal third of hydranth.
*S. linvillei** Hargitt. Shallow water. S.

17. *Cladocoryne*. Perisarc irregularly annulate; colony 2-4mm. high, arising from a reticulate hydrorhiza.
C. sargassensis Hargitt. fig. 81. On *Sargassum*. S.

18. *Corynitis*. Colonial; not branched; tentacles spirally arranged, larger distally; on mussel-shells.
C. agassizi McCr. figs. 3, 4. N. S.

19. EUDENDRIIDÆ. Only genus. *Eudendrium* Ehrenberg 20

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*Until the characters of the polyp of McCrady's *Corynitis* are worked out, it seems best to retain this form in *Syncoryne*. Hargitt's remarks on these genera ('08) are important.

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20. *Eudendrium*. Pedicels of hydranths annulate throughout; hydranths rose color; male gonophores 2-3 chambered; colonies 5 in. high.
E. dispar Ag. N. S. Shallow to 40 fath.

20. *Eudendrium*. Pedicels annulate proximally and distally; hydranths vermillion; male gonophores 2-3 chambered; colonies 4-6 in. high.
E. ramosum Ehr. N. S. Shallow to 400 fath.

20. *Eudendrium*. Pedicels of hydranths annulate only proximally, of gonophoral hydranths throughout; hydranths bright red; male gonophores 4-5 chambered, borne on abortive hydranths (with tentacles); colonies 5 in. high. *E. carneum* Clarke. S. Shallow

20. *Eudendrium*. Pedicels annulate only proximally; hydranths grayish olive; gonophores arising from abortive hydranths, male gonophores 2-chambered; colonies 8mm. high. *E. capillare* Alder. N. S. Shallow

20. *Eudendrium*. Pedicels very slender, not decidedly annulate; hydranths white; gonophores on hydranths with tentacles; male gonophores 2-3 chambered; colonies 6mm. high.
E. album Nutting. fig. 11. N. S. Shallow

21. BOUGAINVILLEIDÆ. Colony with horny perisarc.
Bougainvillea Lesson 22.

21. BOUGAINVILLEIDÆ. Colony with gelatinous perisarc. *Perigonimus* Sars 23

22. *Bougainvillea*. Proboscis small; 15-20 tentacles; colony 2 in. high.
B. superciliaris Ag. fig. 9. N. S. Shore to 10 fath.

22. *Bougainvillea*. Proboscis conspicuous, conical; tentacles about 12; colonies 3-6 in. high, may be 12 in.
B. carolinensis McCr. fig. 7. S. Shallow

23. *Perigonimus*. 6mm. high, branching; flesh-colored; occurred on spider crabs.
P. jonesii Osborn and Hargitt. fig. 16. N. S.

24. PODOCORYNIDÆ. Incrusting base covered with chit-

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inous perisarc; medusoid buds or rudimentary free medusæ with rudimentary tentacles; without mouth.
Stylactis Allman 25

24. PODOCORYNIDÆ. Incrusting base covered with naked flesh; medusæ free swimming, with mouth and well-developed tentacles. *Podocoryne* Sars 26

25. *Stylactis*. Colony 18-25mm. high, on snail shells; color variable; tentacles 18 to 25; free medusæ.
S. hooperi Sigerfoos. fig. 8. S.

26. *Podocoryne*. Colony 4mm. high; tentacles about 12; in reproductive hydranths 4-6; white to flesh color; on shells accompanied by hermit crabs.
P. carnea Sars. fig. 10. N. Shallow.

27. HYDRACTINIIDÆ. Feeding polyps with well-developed tentacles; reproductive with reduced tentacles and medusoid buds; spiral polyps without tentacles, tips with numerous cnidæ; incrusting base with jagged spines. *Hydractinia* Van Beneden 28

28. *Hydractinia*. Colony about 6mm. high; tentacles numerous; on piles and shells occupied by hermit crabs. *H. echinata* (Flem.) N. S. Shore to 60 fath.

29. PENNARIIDÆ. Colony branching, with horny perisarc; reproductive buds few, arising distal to the basal tentacles. *Pennaria* Goldfuss 30

29. PENNARIIDÆ. Hydranth only known; medusæ buds numerous. *Acaulis* Stimpson 31

30. *Pennaria*. Colony 4-10 in. high; branches annulate; stems brown, hydranth vermillion; about 12 tentacles in basal whorl.
P. tiarella McCr. figs. 5, 6. N. S. Low to 10 fath.

31. *Acaulis*. Hydranth about 12mm. long; basal tentacles eight, distal numerous.
A. primarius Stm. N. Low to 5 fath.

32. CORYMORPHIDÆ. Solitary; base of polyp with fleshy processes imbedded in sea bottom; distal tentacles numerous. *Corymorpha* Sars 33

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33. *Corymorpha*. Polyps large, up to 6 in.; bright pink or flesh-color. *C. pendula* Ag. fig. 12. N. S. 6-30 fath.

34. HYBOCODONTIDÆ. Distal tentacles short, in two series; medusa, when liberated, with four small tentacles. *Ectopleura* Ag. 35

34. HYBOCODONTIDÆ. Solitary, unbranched; distinct hydrorhiza; hydranths large; distal tentacles in two whorls, filiform; medusa, when liberated, with one long tentacle. *Hybocodon* Ag. 36

35. *Ectopleura*. Hydranths pinkish red; about 24 basal and 12 distal tentacles. *E. prolifica* Hargitt. S. On crabs

36. *Hybocodon*. About 2 in. high; stems striate, annulate next to hydranth; two whorls of tentacles around proboscis, 16 in each; orange red.
H. prolifer Ag. figs. 13, 82. N. S. Low water

37. TUBULARIIDÆ. Single hydranths with stems free; proboscis long; medusæ buds long, terete, just above proximal tentacles. *Hypolytus* Murbach 38

37. TUBULARIIDÆ. Hydroids fixed by hydrorhiza; a peculiar larva (actinula) escapes from the modified medusa buds. Species not readily distinguished.
Tubularia Linne 39

38. *Hypolytus*. About 12 to 16 proximal tentacles.
H. peregrinus Murbach. fig. 17. S.

39. *Tubularia*. Sessile medusæ with distinct radial canals; colony unbranched; stems often annulate; proximal tentacles 30-40; gonophores in dense racemes; bright scarlet; height 8. in.
T. couthouyi Ag. N. S. Shallow to 30 feet, often in brackish water

39. *Tubularia*. Sessile medusæ without distinct radial canals; and with conical apical processes; stem much annulate; colony bushy; 25-35 mm. high; 16-20 proximal tentacles; hydranths scarlet; gonophores in dense clusters.
T. larynx Ellis and Solander. N. S. Shallow

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39. *Tubularia*. Medusa buds as in last; stems white, not much annulate; colony branched, hydranths rose red; gonophores in dense clusters; height up to 6 or 7 in. *T. spectabilis* Ag. N. S. Shallow

39. *Tubularia*. Medusa buds and perisarc much as in last; colony branched; 1 in. high. *T. tenella* (Ag.) fig. 15. N. S. Low to 40 fath.

39. *Tubularia*. Medusa buds without radial canals, apical process of female flattened; stems white, hydranths rose red; 20-24 proximal tentacles; colony little branched, in tufts 3-4 in. high; readily distinguished from *T. spectabilis* by the female gonophores. *T. crocea* (Ag.) fig. 14. N. S. Low to 6 fath.

HYDRARIÆ.

40. No perisarc; tentacles in a simple whorl; no medusæ buds; inhabitants of fresh water. *Hydra* Linne 41

41. *Hydra*. Color green. *H. viridis*

41. *Hydra*. Color brownish. *H. fusca*

CAMPANULARIÆ.

42. Hydrotheca deep, with pedicel.

42. Hydrothecæ reduced to small disc-like cups (**hydrophores**) usually pedicillate, sometimes sessile on stem. HALECIIDÆ 73

42. Hydrothecæ sessile and joined by side to stem. 45

42. Colony sponge-like; stems arising from a disc-like base and consisting of an intricate mass of axial siphon-like tubes, from which arise elongate cylindrical hydrothecæ, the whole cemented together. *Keratosum* Hargitt 96

43. Hydrotheca without operculum. 44

43. Hydrotheca capable of closure by ring of small teeth (operculum) which meet over the top. CAMPANULINIDÆ 72

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44. Hydrotheca bell-shaped, a septum separating its cavity from that of the pedicel. CAMPANULARIIDÆ 48

44. Hydrotheca ovoid, roughened externally by circular ridges; gonophores in the form of sporosacs just beneath the hydranths, giving rise to planulæ. CALYPTOSPADICIDÆ 46

44. Hydrotheca tubular, no septum. LAFŒIDÆ 77

45. Hydrothecæ on both sides of the stem. SERTULARIIDÆ 81

45. Hydrothecæ on only one side of the stem. PLUMULARIIDÆ 90

46. CALYPTOSPADICIDÆ. Tentacles filiform, in a single whorl at the base of the conical proboscis. *Calyptospadix* Clarke 47

47. *Calyptospadix*. Three or four inches total length; female gonophores and planulæ blue. *C. cerulea* Clarke fig. 88. Littoral. S.

48. CAMPANULARIIDÆ. (Genera and species very difficult to separate except by aid of reproductive history. The following based on Nutting and chiefly applicable to forms south of Cape Cod.)
Stem regularly branched. 51

48. CAMPANULARIIDÆ. Stem not regularly branched. 49

49. Hydrothecæ on long pedicels. 50

49. Hydrothecæ on short pedicels, tubular; margins of hydrothecæ entire, not toothed. *Hebella* Allman 71

50. Hydrotheca toothed; free medusa with four marginal tentacles at birth. *Clytia* Lamouroux 52

50. Hydrotheca entire or toothed; no medusæ; reproduction by planulæ developed in the gonangium. *Campanularia* Lamarck 55

51. No free medusæ; planulæ developed within the gonagium; hydrothecæ entire or toothed. *Campanularia* Lamarck 55

51. Free medusæ with 16+ marginal tentacles with

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statocysts at base; hydrotheca entire or toothed.
Obelia Peron et Lesueur 63

51. No free medusæ; mature gonangia bearing medusa-like bodies at tip; hydrothecæ toothed.
Gonothyraea Allman 70

52. *Clytia*. Teeth of hydrotheca sharp. 53

52. *Clytia*. Teeth of hydrotheca regularly rounded. 54

53. Hydrotheca bell-shaped; teeth about 14; pedicels long; gonothecæ annulate.
C. bicophora Ag. fig. 18. N. S. Shore to 25 fath.

53. Hydrothecæ bell-shaped; teeth 10 to 12; pedicels long; gonothecæ annulate.
*C. johnstoni** (Alder) Hincks. fig. 22. N.

53. Hydrotheca small, cylindrical; teeth about 10; pedicels shorter; gonothecæ smooth.
C. cylindrica Ag. N. S. Shore to 25 fath.

54. Hydrothecæ large, bell-shaped or triangular; pedicels short. *C. nolliformis* (McCrady) fig. 19. S.

54. Hydrothecæ very large, cylindrical, bottom hemispherical; gonothecæ annulate.
C. grayi Nutting. fig. 20. S. 30 fath.

55. *Campanularia*. Colony not branched; pedicels and gonothecæ arising from hydrorhiza. 56

55. *Campanularia*. Colony branched. 59

56. Hydrothecæ entire. 57

56. Hydrothecæ toothed. 58

57. Hydrothecæ deep bell-shaped; pedicels annulate throughout; gonothecæ smooth or wrinkled.
C. poterium Ag. fig. 25. N. S. Low water to 23 fath.

57. Hydrothecæ deep bell-shaped; pedicels twisted, annulate only distally; gonotheca deeply annulate.
C. integra McGillivray. fig. 24. N.

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*The form reported by Hargitt from Woods Hole as *C. volubilis* does not agree with English figures of that species, but is more like *C. johnstoni*.

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57. Hydrotheca elongate, sub-cylindrical, stems annulate above each pedicel, pedicels usually annulate throughout. *C. fragilis* Hincks. fig. 36. N.

58. Hydrothecæ deep bell-shaped, lined longitudinally; teeth square on top; pedicels annulate distally; gonothecæ ringed. *C. hincksii* Alder. fig. 26. S. 15 fath.

58. Hydrothecæ deep tubular; teeth shallow, rounded; pedicels spirally twisted; gonothecæ smooth, flask-shaped, narrower distally.
C. volubilis (L.) Alder. fig. 21. N. S. Low water to 100 fath.

59. Hydrothecæ toothed. 60

59. Hydrothecæ entire. 62

60. Stem fascicled: pedicels in verticils; hydrothecæ bell-shaped; teeth sharp or rounded.
C. verticillata (L.) Lamarck. fig. 23. N. S. 4 to 45 fath.

60. Stem not fascicled; pedicels not verticellate. 61

61. Teeth of tubular hydrothecæ 8 to 10, castellate or bimucronate; pedicels long, annulate at ends or throughout; gonophores in axils.
C. neglecta (Alder) Hincks. fig. 27. N. S. Shallow.

61. Teeth of tubular hydrothecæ 12 to 14, acute; pedicels very long, annulate at ends.
C. edwardsii Nutting. fig. 31. S. On piles.

61. Teeth of bell-shaped hydrotheca 8 to 10; pedicels and stems extensively annulate.
C. minuta Nutting. fig. 37. S. Shallow.

62. Gonothecæ with peculiar latero-terminal aperture; hydrothecæ bell-shaped; pedicels annulate.
C. calceolifera Hincks. fig. 28. S. Shallow.

62. Gonothecæ normal; branches verticillate; pedicels smooth or ringed in middle; hydrothcæ deep bell-shaped. *C. amphora* (Ag.) fig. 29. N. S. Shallow.

62. Gonothecæ normal; main stem flexuose; pedicels alternate, ringed throughout; hydrothecæ bell-shaped. *C. flexuosa* Hinks. fig. 30. N. Shallow.

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62. Gonothecæ normal; stem angulate, with alternate ringed pedicels; stems ringed above each pedicel; hydrothecæ bell-shaped; gonothecæ on hydrorhiza.
C. angulata Hincks. N. S. Shallow.

63. *Obelia*. Margin of hydrothecæ entire; stem not fascicled. 64

63. *Obelia*. Margin of hydrothecæ toothed; stem fascicled. 67

64. Colony a long, central stem with sub-verticillate branches, these palmately branched. 66

64. Irregularly branched, branches often branching in turn; hydrothecæ large, deeply campanulate.
O. dichotoma (L.) Hincks. N. S. Tide pools to 10 fath.

64. Usually a geniculate stem, giving off alternate pedicels. 65

65. Stem very stout; pedicels short.
O. geniculata (L.) Allman. fig. 35. N. S. Shore to 40 fath.

65. Stem slender; pedicels longer.
O. congdoni Hargitt. fig. 91. S. On gulfweed.

66. Hydrothecæ triangular; pedicels usually with more than 6 rings.
O. flabellata Hincks. fig. 40. S. Shore to 5 fath.

66. Hydrothecæ deeper, sub-triangular; pedicels often with more than 6 rings. *O. commissuralis* McCrady. fig. 34. N. S. Piles and floating timber.

67. Teeth of hydrothecæ bimucronate or castellate. 68

67. Teeth very shallow undulations.
O. longissima (Pallas) Hincks. fig. 39. N. S. 3 fath.

68. Hydrothecæ deep, with vertical lines. 69

68. Hydrothecæ triangular, without vertical lines.
O. gelatinosa (Pallas) Hincks. fig. 41. N. S. Low to 20 fath.

69. Pedicels with 6 to 15 rings; hydrothecæ deep tubular. *O. bicuspidata* Clarke. fig. 32. S. 3 to 19 fath.

69. Pedicels with 3 to 6 rings; hydrothecæ shorter.
O. bidentata Clarke. fig. 38. S. On piles.

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70. *Gonothyræa*. Hydrothecal teeth flat or bimucronate; pedicels annulate at end; gonothecæ in axils, on ringed pedicels. *G. hyalina* Hincks. N. 10 fath.

70. *Gonothyræa*. Hydrothecal teeth small, rounded; pedicels ringed at ends or throughout; gonothecæ in axils, on ringed pedicels.
G. loveni Allman. fig. 42. S. Shallow.

70. *Gonothyræa*. Hydrotheca deep, tubular, with about 10 long, pointed teeth; gonothecæ on stems and on hydrorhiza. *G. gracilis* (Sars) Allman. fig. 33. N.

71. *Hebella*. Hydrothecæ in pairs, doubly curved; usually parasitic on *Sertularia cornicina*.
H. calcarata (A. Ag.) fig. 43. S.

71. *Hebella*. Hydrothecæ scattered, not doubly curved; parasitic on various hydroids.
H. pygmæa (Alder.) fig. 44. N. S. Low water to 8 fath.

72. CAMPANULINIDÆ. Stem annulate throughout; opercular teeth not sharply marked off from hydrotheca; gonothecæ borne on ringed pedicels.
*Opercularella lacerata** Hincks. fig. 87. S. On piles.

72. CAMPANULINIDÆ. Stem not ringed throughout; colony branched; gonothecæ on hydrocaulus; opercular teeth sharply distinct from hydrotheca.
Lovenella grandis Nutting. fig. 46*a*. N. S.

72. *Campanulinidæ*. Stem a creeping rootstalk on other hydroids, giving off ringed pedicels; opercular teeth distinct; gonothecæ on hydrorhiza.
Calycella syringa† (L.) fig. 45. N. S.

73. HALECIIDÆ. Hydrophores with even margins, often surrounded by a circle of bead-like dots.
Halecium Oken. 74

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* *O. pumila* Clarke is hardly to be distinguished from this; it is reported from both sides of Cape Cod.

† *C. nuttingii* Hargitt is not easily recognized as distinct from *C. syringa*.

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74. *Halecium*. Hydrophores sessile, on shoulder of internode; colony large, up to 2 feet high.
H. articulosum Clarke. fig. 47. S. 31 fath.

74. Hydrophores on distinct pedicels. 75

75. Stem not fascicled, branching irregularly, annulate, internodes long. *H. tenellum* Hincks. fig. 48. N. S.

75. Stem fascicled. 76

76. Female gonotheca spinose.
H. muricatum (E. and S.) fig. 46. N.

76. Female gonotheca smooth, mitten-shaped, aperture lateral. *H. beani* (Johnston.) fig. 50. N. S.

76. Female gonotheca smooth, aperture terminal.
H. halecinum L. fig. 54. N. S. Shallow.

77. LAFŒIDÆ. Hydrothecæ arising from an upright, fascicled stem, adnate for most of their length.
Salacia Lamouroux 78

77. LAFŒIDÆ. Hydrothecæ arising from creeping, interlacing rootstalk, to which they are adnate for a part of their length. *Filellum* Hincks 79

77. LAFŒIDÆ. Hydrothecæ arising from a creeping or upright fascicled stem, free. *Lafœa** Lamouroux 80

78. *Salacia*. Horn-colored; hydrothecæ in 4 or 5 longitudinal rows, margins smooth.
S. abietina (Sars) Hincks. fig. 53. N.

79. *Filellum*. Hydrothecæ adnate for about two-thirds their length; common on *Sertulariæ*.
F. serpens (Hassall) Hincks. fig. 57. N.

80. *Lafœa*. Hydrothecæ slender; pedicels with 3 or 4 rings. *L. dumosa* (Fleming) Sars. fig. 52. N. S.

80. Hydrothecæ slender; pedicels with 3 or 4 rings.
L. fruticosa Sars. fig. 55. N.

80. *Lafœa*. Hydrothecæ slender; pedicels waved or twisted. *L. gracillima* (Alder.) fig. 51. N.

* The sexual form of Lafœa (fig. 56) was long known as Coppina arcta.

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81. SERTULARIIDÆ. Hydrothecæ in strictly opposite pairs, a pair to each internode. 82

81. SERTULARIIDÆ. Hydrothecæ strictly opposite, more than a pair to an internode; margins bilabiate, with a 2 or 3 flapped operculum. *Pasythea* Lamouroux 84

81. SERTULARIIDÆ. Hydrothecæ strictly alternate. 83

81. SERTULARIIDÆ. Hydrothecæ sub-opposite, more than a pair to an internode. *Thuiaria* Flemming 85

82. Operculum of hydrotheca, when present, in two pieces; gonothecæ with simple opening and without marsupium. *Sertularia L.* 86

82. Operculum, when present, a single piece; gonotheca spined and cleft distally, with marsupium. *Diphasia* Agassiz 87

83. Hydrothecæ on opposite sides of stems and branches; gonothecæ usually annulate. *Sertularella* Gray 88

83. Hydrothecæ on one side of branch, turned alternately to right and left. *Hydrallmannia* Hincks. 89

84. *Pasythea*. 4 to 9mm. high; 1 to 5 pairs of hydrothecæ to node. *P. nodosa* Hargitt. fig. 89. S. On gulfweed.

85. *Thuiaria*. Gonothecæ with 2 lateral projections; distal third of hydrothecæ free.
T. argentea (E. and S.) figs. 58, 59. N. S. Low to 100 fath.

85. *Thuiaria*. Gonothecæ with two lateral projections; hydrothecæ all immersed in stem.
T. cupressina (L.) fig. 60. N. S. Low to 110 fath.

85. *Thuiaria*. Gonothecæ ovate, without lateral spines; hydrothecæ sub-opposite, almost entirely immersed.
T. thuja (L.) Flemming, fig. 61. N. S.

85. *Thuiaria*. Gonothecæ ovate, without lateral spines; hydrothecæ sub-opposite, about half free; distal portion contracted, aperture small.
T. filicula (E. and S.) fig. 65. N.

86. *Sertularia*. Hydrothecæ of a pair scarcely touching each other in front; gonothecæ on stout pedicels.
S. pumila (L.) fig. 62. N. S. Between tides.

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86. *Sertularia*. Hydrothecæ in contact two-thirds their length; width of pair at base less than distance from base to node below; gonothecæ at base of stem, annulate. *S. complexa* Clarke. fig. 64. S. Shallow.

86. *Sertularia*. Hydrothecæ in contact two-thirds their length; width at base about equal to distance from node. *S. cornicina* McCrady. fig. 63. S. 8 fath.

86. *Sertularia*. Hydrothecæ alternate and distant on stem, opposite on branches, and contiguous for half to nearly entire length; gonothecæ unknown.
S. versluysii Nutting. fig. 86. S. On gulfweed.

87. *Diphasia*. Width of a pair of hydrothecæ about equal to their height; male gonothecæ with 4 terminal spines, female with 4 long processes at tip.
D. fallax (Johnston) Ag. fig. 66. N. S. Shallow to 23 fath.

87. *Diphasia*. Width of a pair about two-thirds their height; hydrothecæ bent outward sharply at middle; male gonothecæ with longitudinal ridges and terminal spines, female with 2 large and several small processes.
D. rosacea (L.) Ag. fig. 68. N. S. Low to 10 fath.

87. *Diphasia*. Proportions of hydrothecæ much as in last, not sharply bent; male gonothecæ compressed, short, broad distally; female with numerous irregular distal spines. *D. tamarisca* (L.) Ag. fig. 67. N.

88. *Sertularella*. Hydrothecal margin without teeth or operculum; gonothecæ wrinkled.
S. abietina (L.) figs. 69, 70. N. S.

88. *Sertularella*. Hydrothecal margin 3-toothed; gonothecæ strongly ringed, orifice narrow.
S. tricuspidata Alder. fig. 73. N. S. Low to 23 fath.

88. *Sertularella*. Hydrothecæ 4-toothed, large, smooth or wrinkled; gonothecæ annulate distally, aperture 2-toothed.
S. gayi (Lamx.) Hincks. fig. 79. N. S. 25 fath.

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88. *Sertularella*. Hydrothecæ obscurely 4-toothed, deeply wrinkled transversely; gonothecæ very large, wrinkled.
S. rugosa (L.) Gray. fig. 75. N. S. Shallow to 25 fath.

88. *Sertularella*. Hydrothecæ smooth, 4-toothed; gonothecæ corrugate, with 4-toothed opening.
S. polyzonias (L.) Gray. fig. 80. N. S. Low to 25 fath.

89. *Hydrallmannia*. Hydrothecæ only on branches, several to an internode, narrowed distally, with operculum.
H. falcata (L.) Hincks. fig. 77. N. S. Low to 150 fath.

90. PLUMULARIIDÆ.* No corbulæ; nematophores trumpet-shaped, not immovably fixed to hydrothecæ.

90. PLUMULARIIDÆ. No corbulæ; nematophores fixed to hydrocladus near free end of hydrothecæ; mouth of hydrotheca serrate. *Thecocapsus* Nutting 92

90. PLUMULARIIDÆ. Corbulæ present; three nematophores on each hydrotheca; hydrothecal margin dentate. *Aglaophenia* Lamx. 95

91. Branching pinnate; some or all hydrocladia forked; usually a cluster of simple stems. *Schizotricha* Allman 93

91. Verticillate or scattered branches; gonangia usually in axils of hydrocladia. *Antennularia* Lamarck 94

92. *Thecocapus*. One mesal nematophore; thickening of internodes evident; corbulæ open, of numerous distant leaves; colony about 18 inches high.
T. myriophyllum (L.) Nutting. fig. 78. N.

93. *Schizotricha*. A hydrotheca in the axil of each hydrocladium; one nematophore in each internode; gonangia pedicillate.
S. tenella (Verrill) Nutting. fig. 76. S. 8 to 10 fath.

* The hydrocladia are the branchlets which bear the hydrothecae; nematophores are minute cups (containing structures known as sarcostyles capable of enormous extension) attached to hydrothecæ, stems, etc. In some Plumulariidæ the gonangia are enclosed in podlike capsules (corbulae) formed of modified branches.

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93. *Schizotricha.* Stem fascicled, each hydrocladium bearing a hydrotheca on the distal half of the long internodes; 3 or 4 nematophores to each internode; gonangia in pairs, almost sessile.

S. gracillima (Sars) Nutting. figs. 74, 85.
N. S. Shallow to 200 fath.

94. *Antennularia.* A node between first hydrotheca on hydrocladium and the stem; gonothecæ on base of hydrocladia.

A. antennina (L.) Johnston. fig. 72. S. 60 fath.

94. *Antennularia.* No node between first hydrotheca and stem; at least 2 nodes between hydrothecæ; gonothecæ in axils.

A. americana Nutting. fig. 71. S. 50 to 120 fath.

95. *Aglaophenia.* One-fourth to one-half inch high; pinnæ alternate; hydrothecæ closely crowded.

A. minuta Fewkes. fig. 84. S. Floating algæ and 233 fath.

96. *Keratosum.* Hydrothecæ more or less curved and interspersed with nematothecæ; gonospores, hydranths, etc., unknown.

K. complexum Hargitt. fig. 90. S. Shallow.

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BIBLIOGRAPHY.

Agassiz, A. 1865. North American Acalephæ. Illustrated Catalogue Mus. Comp. Zool., No. 2.

Agassiz, L. 1849. Contributions to the natural history of the Acalephæ of North America. Memoirs Amer. Acad. Arts and Sci., 4.

1862. Contributions to the natural history of the United States. Vol. 4 contains the Hydrozoa.

Allman, G. J. 1871. A monograph of the gymnoblastic or tubularian hydroids. London, Ray Society.

Clarke, S. F. 1875. Descriptions of new and rare Hydroids from the New England Coast. Trans. Conn. Acad., 3, p. 58, 1 pl.

1882. New Hydroids from Chesapeake Bay. Memoirs Boston Society Nat. Hist., 3, p. 135, 3 pls.

Congdon, E. D. 1907. The Hydroids of Bermuda. Proc. Amer. Arts and Sci., 42, p. 463.

Fewkes, J. W. 1880. Report on the Acalephæ in Report on the results of dredging, under the supervision of Alexander Agassiz in the Caribbean Sea, etc. Bull. Mus. Comp. Zool., 8, p. 127, 4 pls.

1881. Studies of the jelly fishes of Narragansett Bay. Bull. Mus. Comp. Zool., 3, p. 141, 10 pls.

1882a. Exploration of the surface fauna of the Gulf Stream. Bull. Mus. Comp. Zool., 9, p. 129, 7 pls.

1882b. On the Acalephæ of the east coast of New England. Bull. Mus. Comp. Zool., 9, p. 291, 1 pl.

1891. An aid to the collector of the Coelenterata and Echinodermata of New England. Bull. Essex Inst., 23, p. 1.

Hargitt, C. W. 1901. Synopses of North American Invertebrates. XV. The Hydromedusæ (3 parts) American Naturalist, 35.

1904. The Medusæ of the Woods Hole Region. Bull. U. S. Bureau of fisheries, 24, p. 21, 7 pls.

Digitized by Google

1904b. Notes on a hitherto undescribed Hydroid from Long Island Sound. Biol. Bull., 7, p. 251.

1905. Notes on the variations of Rhegmatodes. Biol. Bull., 9.

1908. Notes on a few Cœlenterates of Woods Hole. Biol. Bull., 14.

1909. New and little known Hydroids of Woods Hole. Biol. Bull., 17, p. 369.

Hargitt, G. T. 1903. Regeneration in Hydromedusæ. University (of Nebraska) Studies, 3.

Hincks, T. 1868. A history of the British Hydroid Zoophytes. 2 vols. London.

Johnston, G. 1838. History of the British Zoophytes, Edinburgh. 1847. Same, second edition, London.

McCrady, J. 1858. Gymnophthalmata of Charleston harbor. Proceedings Elliott Society, 1.

Mayer, A. G. 1900a. Some medusæ from the Tortugas, Florida. Bull. Mus. Comp. Zool., 37, 44 pls.

1900b. New and little known medusæ from the Western Atlantic. Bull. Mus. Comp. Zool., 37, 6 pls.

Murbach, L. 1895. Note on the life history of Gonionemus. Journal of Morphology, 11.

Nutting, C. C. 1900. American Hydroids, Part I. The Plumulariidæ. U. S. National Museum, Special Bull.

1901. The Hydroids of the Woods Hole region. Bull. U. S. Fish Commission for 1899, p. 324.

1904. American Hydroids, Part II. The Sertulariidæ. U. S. National Museum, Special Bull.

Osborn, H. L., and Hargitt, C. W. 1894. Perigonimus jonesii. American Naturalist, 28.

Perkins, H. F. 1902. The development of Goniomema murbachii. Proc. Acad. Nat. Sci., Philadelphia.

Sigerfoos, C. P. 1899. A new Hydroid (Stylactis hooperi) Amer. Nat., 33, p. 801.

Stimpson, W. 1853. Synopsis of the marine Invertebrata of Grand Menan. Smithsonian Contributions to Knowledge.

Digitized by Google

Verrill, A. E. 1873–74. Results of recent dredging expeditions on the coast of New England. Amer. Jour. Sci. and Arts, 5 to 7 (7 numbers), 5 pls.

1874a. In Verrill and Smith. Invertebrate animals of Vineyard Sound. Report U. S. Fish Commission for 1871–72, 38 pls.

1874b. In Smith and Harger. Dredgings in the region of St. George's Banks in 1872. Trans. Conn. Acad. Sci., 3, p. 1, 8 pls.

1874c. Explorations of Casco Bay by the U. S. Fish Commission in 1873. Proc. Amer. Assoc. Adv. Sci., p. 340, 6 pls.

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WET AND DRY DIFFERENTIATION OF IGNEOUS ROCKS.

By A. C. Lane.

In the old quarterly reviews such as Macaulay used to write it was customary for the reviewer to use some recent book or books upon the subject merely as a text, and after calling attention to them proceed to develop his own point of view. I am inclined to think this might be a good form for scientific papers. At any rate, it appeals to me as a means of introducing some observations of my own upon the differentiation of igneous rocks.

First to be mentioned is one by the leader in this line of research, Vogt.* When Vogt in the first reference cited, states his "belief" that magmatic water has not in general an important influence upon the order of crystallization he goes farther than theory would warrant and the facts I later gave indicated, and differs materially from the conclusion indicated by the results of other investigators. Day † calls attention to the fact that small proportions of impurity may have a much larger effect upon the melting point. The work of Day, Wright and others of the Geo-physical Laboratory in Washington is of fundamental value to any one who would study the subject, though we cannot agree with Day at all that there is no profit in determining the point of melting and solidifying of natural minerals, or in watching for the moment when minerals begin to sag and run.

The fact is, the relation between the work of the geologist, and that of Day and his associates, is something like that between the preliminary and final surveys of a railroad. The work of the preliminary party with barometer, etc., is rough, almost beyond comparison with that of the final party, and they must use the work of the final party as the basis for their work. Nevertheless, their work is of the utmost value in determining where the final party shall go, and it is only in a very easy country

* Über Anchi-eütektische und Anchi-monomineralische Eruptivgesteine, p. 19.

† Program 22d Winter Meeting, Geol. Soc. Am. 1909, p. 27.

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that a good final survey can be run without preliminary work. Now Day himself has called attention to the fact that in the study of silicates we are dealing with a very complicated problem; that the topography, if one may use a figure of speech of the surfaces of fusion of a rock, is extremely mountainous and rocky, so that at present he is utterly unable to master the problem in its generality.

The same difficulty always arises in applying mathematical physics. Mathematics deals with ideal conditions which are never realized in the real work, and it is the province of the physicist to grasp by a sort of intuition those factors which are likely to be the important ones, and then work out the ideal and abstract mathematical theory for those cases. Then upon applying these ideals to the real facts in nature, it will be found in many cases that there is a sufficient overlapping to make the ideal results of real value. In just such cases it would seem that the work of the geologists in suggesting what had actually taken place and what lines of research were most likely to be similar to those of nature would be of value, and it is my hope that my work on grain and that of this paper may be to Day's work in the nature of reconnaissance surveys. Doelter * and Harker † both commented upon the fact (which I readily grant) that in my work on the theory of the variation of the coarseness of grain of rocks, I have considered the loss of heat and the conduction and diffusion of the same to the neglect of other important factors, such as undercooling, absorption of latent heat. It will be found that in my very first paper ‡ and elsewhere I have noted that fact and have always in my application of the theory found that considerable correction was due to factors for which I have not yet published a mathematical treatment. I have a certain way of handling some of them, but I am not satisfied with its theoretical validity. And it is true that in many cases one can see about what kind of effect will be produced by the neglected factors when no rigid mathematical treatment can be given. Moreover, as I have remarked, not merely the progres-

* Petrogenesis, p. 45.

† The Natural History of the Igneous Rocks, p. 220,

‡ Isle Royale. Report Michigan Geol. Survey, Vol. VI, Part I, p. 107.

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sive loss of heat alone, but that of mineralizers or any other factors in crystallization whose change in time depends on spatial transfer must follow much the same mathematical laws. Thus I think the theory already developed is likely to fit the facts closer than Harker is inclined to believe and I do find a "significant" connection between fact and theory.

For instance, it is a general principle that in any such body the contour curves connecting parts in a similar state tend to smooth out in the course of time.* There is, we may say, peneplanation. Thus if there are cooler enclosures in a mass of plutonic rock, the fragments thus enclosed will heat up, or, at any rate, cool more slowly until the whole mass is at about the same temperature, and cooling at about the same rate. Crystallization around such enclosures during the time before they have attained a condition of equilibrium with the rest of the rock will then be liable to be, and often is, coarser. In the same way it is very true that the giving out of latent heat by crystallization is an important factor in retarding the cooling of rock as Harker in his very valuable work has emphasized. But it is also true, as Day and his associates have remarked, that this effect can be considered very much the same as though the specific heat varied very much at and near the temperature of crystallization. Now we know that in any case the specific heat of a rock varies and though a^2 is usually taken as constant in the equation $D_t u = a^2 D_x^2 u$, it is really not so. a^2 is equal to the conductivity k divided by the specific heat c. But we can get some idea of what kind of effect this will produce and still use the same diagrams for the loss of heat in a cooling sheet if $a = f(u)$, in case this variation in a^2 is dependent (as it very generally is) upon u simply — not upon x_2 and t, by replacing u with some other function w, so connected with u that a^2 really is a constant $= f(u_0)$ for w as a function of t and x, and the equations which have been found will then really hold. We shall have as a second problem to find what u is in terms of w. If then we take the ordinates which represent w and put along side the curves connecting w and x others connecting w and u,

* This follows as a physical interpretation of the equation $D_t u = a^2 D_x^2 u$.

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we may be able to trace the relations of u and x. But I am not satisfied this method is really valid. It can probably be used if the variations in diffusivity are not too great. Certain important consequences will appear at once.

The method developed of showing that the grain is proportionate to the distance from the margin in the very earliest stages of cooling, developed in Vol. VI of the Michigan Geological Survey, by changing the scale of the phenomena, is also applicable even though the diffusivity is not absolutely constant. But in undercooling and devitrification and the grain produced thereby, other factors become of great importance.

For instance, if various curves of loss of w for different values of x have the same value of w, they will also have the same slope for u *so long as w is a function of u, and not of x and t* or in terms of grain such a variation of diffusivity whether due to variation in conductivity or in specific heat capacity, or what is its equivalent, absorption of heat or emission thereof in process of crystallization, will not affect the theory of grain, which I have developed *so far as the belts* of equal grain are concerned. Now really the most important result of my studies of general interest (for I have never supposed that the numerical values of the increase of augite grain found in the copper-bearing rocks would be likely to be exactly applicable elsewhere and undercooling unquestionably plays a large rôle in the feldspar grain) is in my conclusion, that the superficial or volcanic rocks are liable to flow until they are stiff and on the point of consolidation, and that under those circumstances there is then but little central zone of uniform grain, in the consolidation. If on the other hand, the deep seated or plutonic rocks are liable to be injected at a higher temperature, to be injected in hotter rocks, and to retain mineralizers which tend to bring the crystallization point down much lower, much longer, under these conditions there is likely to be at least a central zone of uniform grain such as is actually shown in intrusive dikes only fifty feet across. Under suitable conditions the grain of a particular mineral may be uniform clear to the margin or even coarser or conceivably coarser in a belt between the center and the margin, and then finer towards the margin. All these conditions are actually realized in nature. So while Harker seems

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to think * that there is no probability of superheating of the magmas, he gives no proof that such is the case, and many facts that point the other way. For instance, he evidently believes in a settling of certain constituents of the plutonic magmas and magmatic differentiation.† Now this could hardly go on unless the magma is somewhat fluid and that depends upon its point of consolidation. But there are a number of other investigations recently which have all pointed one way to a great likelihood of superfusion, especially in the acid or salic magmas. For instance, it has been proved that quartz will only form below 800° centigrade, at which temperature it inverts to tridymite. This follows from the researches of Day and his associates ‡ and also from the brilliant investigations of Brun.§ In fact, from the work of Wright and Larson one can pretty definitely say that the crystallization of the earliest quartz of granite and porphyry took place between 550° and 800° centigrade. That is to say, in the diagram of magmatic zones which I published in 1893 ‖ I got the acid zone somewhat high, for the presence of porphyritic quartz in the quartz porphyries would point to its crystallization at a temperature corresponding to a depth of seventeen to twenty-seven kilometers, or ten to seventeen miles. Now, it is one of the great merits of the recent work of Brun

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* Page 184.

† Soc. cit. p. 319.

‡ Wright and Larson, "Quartz as a Geological Thermometer." Am. Journal Sci.

§ Synthese du Quartz; April, 1908.

Étude sur le Point de Fusion des Mineraux et sur Les Consequences petrographiques et synthetiques qui en resultent, April, 1902.

Quelques sur le Volcanisme, May and June, 1905.

Quelques sur le Volcanisme (second part), Nov., 1906.

Quelques Recherches sur le Volcanisme au Pico de Teyde et au Timanfaya, Feb., 1908.

Quelques Recherches sur le Volcanisme aus Volcans de Java, Feb., 1909.

Quelques Recherches sur le Volcanisme aux Volcans de Java. Le Krakatau, July, 1909.

All from "Archives des Sciences physiques et naturelles."

Verhalten des Schwefels in tatigen Solfataren, Chemiker-Zeitung, 1909.

‖ Bull, G. S. A. "Rôle of originally absorbed gases."

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that he has put the old belief of the French petrographer in mineralizers on a definite basis, and has shown temperatures much above 550° in lavas. On the other hand there are numerous reasons independent of grain for believing with Harker that the crystallization of granite finished below 500°, perhaps as low as 200° to 350° centigrade.* Brun seems to me to emphasize, perhaps too strongly, the anhydrous character of his lavas. It is true that as they exist and as they come forth from the volcano they apparently contain no water, but that is at a temperature of about 639° centigrade, and in the very table referred to I called attention to Bell's blast furnace reaction, by which steam is decomposed by iron (and presumably by ferrous iron) above 639° centigrade in formation of ferric iron. Thus in femic rocks it is quite likely that water molecules should not exist as such above some such temperature. But in ammonic chloride and carbon dioxide and the hydrocarbons which he finds, there are elements of water which may combine together, if the magma is allowed to cool slowly so that they are not in any solid solutions as glass, but under pressure, so they are not allowed to evaporate. Thus there is no reason why magmas and especially granitic magmas not of a femic character should not contain water or hydroxyl, of which indeed the presence of muscovite and hornblendes and epidote as primary constituents would be a proof.

But Brun has also called attention to the presence of other constituents which are liable to be gaseous, particularly chlorine and sulphur as well as CO_2 and hydrocarbons, and ammonic chloride. Now there is every reason for believing that the retention of such constituents will materially lower the fusion point and the consolidation point for some or all of the constituents of the plutonic magma. Just what function they will have, just which constituents will be affected is a question which it seems to me the geologists can help to answer by observations on the order of crystallization and grain of constituents.

I have called attention to the fact that in various surface

* Harker, p. 189.

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lava-flows containing a good deal of soda or in the family where augite occurs and crystalizes after feldspar, that is the basalts and tholeyites, there is a tendency toward a differentiation by which the feldspar rises to the top of the flow, the augite comes in the lower and last consolidated part. It is true also in a series of closely allied flows that the upper part is often noticeably more feldspathic; feldspar being somewhat porphyritic in grouped aggregates, or, in fact, preceding the general consolidation only a short time. I have called attention to this class of differentiation in my paper on the "Magmatic Differentiation

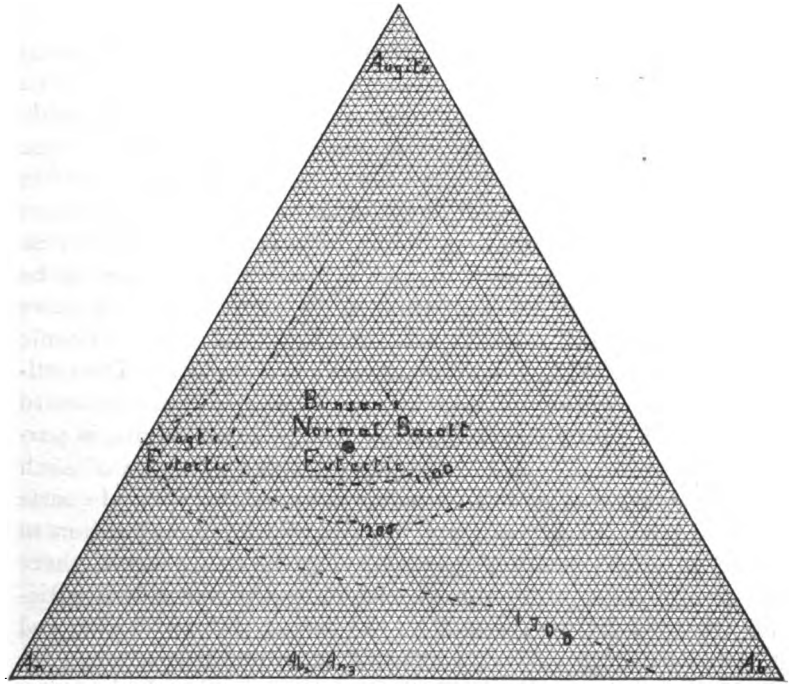

Fig. 1. Suggested eutectic region of a mixture of albite anorthite and augite molecules, in the presence of iron oxide and other impurities, but without water. The augite, without doubt, changes composition. Reckoning back from Bunsen's normal basaltic magma and labradorite, the composition would be 43% SiO 31% ($Al_2O_3Fe_2O_3$) 11% CaO, and 14% MgO, which is a possible pyroxene composition, though low in lime. Much of the iron probably crystallizes separately.

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in the Rocks of the Copper-bearing Series."* A feature of this differentiation is that the last crystallized part of the flow, the positive pole of differentiation, in other words, is not far from the composition of Bunsen's normal basaltic magma. Its proportions of silica to other constituents are pretty close to that of an augite but it does not seem to be really a tendency to become all augite, but rather a mixture of augite and a feldspar of the same acidity, to wit, $Ab_2 An_3$ and it will be noticed that Vogt's investigations of the crystallization of the albite and anorthite series (p. 9, Fig. 2) lead to something like a similar feldspar. In other words, the diagram for augite, albite and anorthite might be somewhat as shown in Fig. 1.

Now, in the case of these lavas there is no question but what the differentiation is a thermal one, and, though affected by the proportions of the various constituents, yet not appreciably affected by the mineralizing agents of gases. I have been accustomed to call this in my mind "dry differentiation" in contradistinction to the differentiation of the quartz feldspar eutectic "wet differentiation," but I have not a doubt that Brun would criticize the latter term, and, if it is used at all, it must be used in the sense of differentiation in the presence of such gases (whether steam or others) as are commonly absorbed in plutonic magmas where there has been no chance of escape. The ordinary course of differentiation in many plutonic rocks is toward a mixture of quartz and feldspar, and many experiments, in particular those of Brun, have shown how the presence of such mineralizing gases tends to promote the crystallization of quartz in heated glass, and probably to retard the crystallization of quartz in slowly cooling magmas. On the other hand, there are certain cases where there seems to be a plutonic differentiation which is entirely parallel to the surface differentiation, and it is to be interpreted as a thermal differentiation with an increase in CaO towards a most fusible rock composed of augite. That such a rock should be most fusible is only natural when we consider how complex the augite molecule is and how, generally speaking, the more constituents the lower the melting

* Bull. Geol. Surv. Am. 1898.

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point.* Now there seems to be no reason, if we consider, as I do in my paper on the "Geological Activity of the Earth's Originally Absorbed Gases," the three factors that keep a magma in fluid state as T, P and M, why this third factor M should always be lost at the same rate. It seems perfectly possible that a magma might be in one case thrust into relatively dry rocks and in another case into relatively wet, another intruded beneath the ocean and another intruded beneath the sand or clays or shales, in one case be the consolidated neck of the volcano with a free chance of escape of gases, in another case enclosed as a laccolite from which gases could only diffuse themselves into the surrounding rocks.

The presence of mineralizers, especially water, seems to promote the solubility of the salic constituents (the quartz and feldspar). Therefore in the case of a magma, when the mineralizers were retained, there would be a tendency to a crystallization of the femic constituent or relatively basic margin, — a very common case.† On the other hand, if mineralizers escaped, there might be a crystallization of less fusible feldspar before a temperature was reached at which the augite could crystallize as in the Keweenawan lavas, and so a femic concentration takes place in the later crystallized part, or at any rate, depending on the proportions of various constituents, a differentiation quite other than would have been the case had the mineralizer been retained. This case is also mentioned by Harker.

All this is a rather long introduction (an "intolerable deal of sack to a half-pennyworth of bread") to a description of two cases where it seems to me there is indication of a "dry" rather than a "wet" (mineralizer-modified) differentiation.

An admirable paper on the Haystack by Emmons in the Journal of Geology ‡ interested me greatly. Though one may not agree entirely with the author's conclusions, his descriptions are so clear that one is able to draw his own inferences from the facts. The author compares it to Mount Johnson, as it seems

* Cf. Day's remarks and the various diagrams published by the Geophysical laboratory at Washington.

† Harker, p. 133.

‡ Journal of Geology, 1906, p. 202.

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to me very acutely and justly, and I am tempted to make a few comments, because while I have not seen the Haystack, I have some unpublished notes on Mount Johnson, which has been very carefully studied by Adams, as to the relative unimportance of magmatic water in differentiation, and both seem to illustrate this thermal differentiation toward augite rather than aqueous differentiation toward pegmatite or feldspathic rock as a last residue.

MOUNT JOHNSON.

First as to my observations on Mount Johnson, where I had the pleasure and profit of the guidance of Prof. J. W. Dresser, and the help of Adams' paper and analyses.* The structure is very simple. Adams interprets it, I think rightly, as a volcanic neck, in which case it might the more readily lose its mineralizers. There is a ring of sediments altered to hornstones, then a narrow, fine grained, ill exposed zone,† then a zone of Laurvikose characterized by large plagioclase crystals up to 90 mm. long. These large border phenocrysts and the rock as a whole have an arrangement parallel to the hillslopes — to the contact. As we go in, the coarse feldspars grow *gradually* smaller, while the hornblende remains fairly uniform throughout. At the centre the rock appears darker, more femic, there is a curious coarse spotted appearance, and even with the naked eye one can see hornblende rims surrounding the augite cores, whereas at the margin it was apparently all hornblende.

The observations are tabulated below. I copy Adams' figure, showing the course of my section. (See Journal of Geology, 1903, p. 255.)

Now from the very narrow fine grained margin, which may until devitrified have been glassy, we may infer a high degree of superfusion, so that in the beginning, before the contact rocks had fully heated up, only a narrow zone congealed and crystallized. The cooling of the zone of slowest cooling just inside, as the contact zone attained its maximum temperature and slowly began to cool was relatively very slow, and at the close of the

* Journal of Geology, 1903, p. 219.

† Possibly a devitrification zone.

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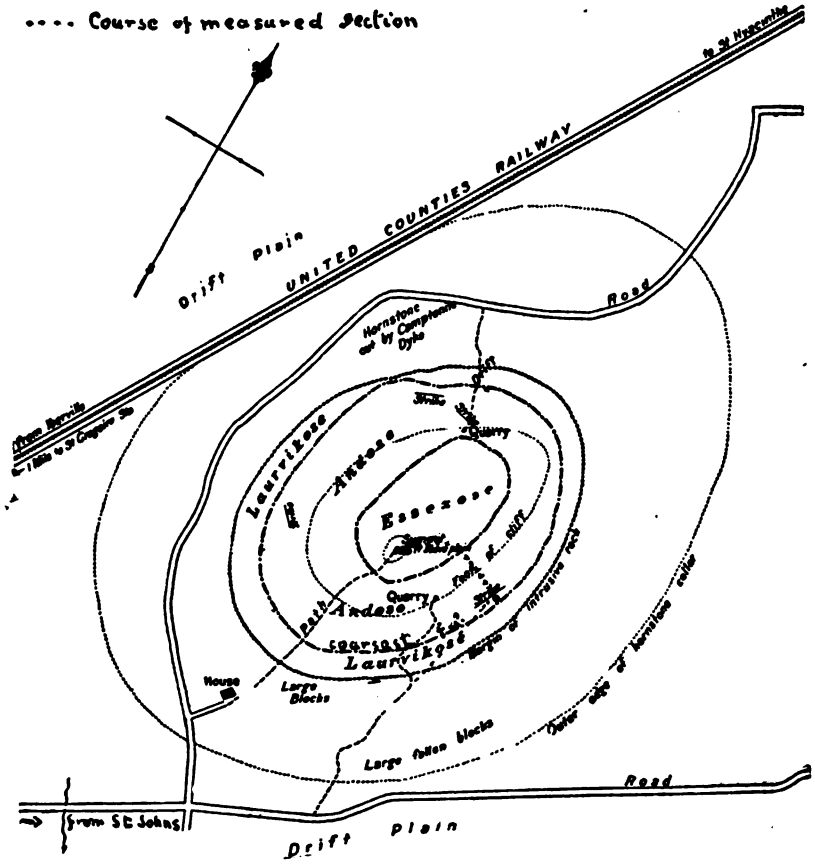

Fig. 2. Map of Mount Johnson, Quebec, after Adams.

eruption that gave a chance for those molecules, which in this magma under the given temperature and pressure conditions were in excess and most ready to crystallize, a chance to migrate to the margin, as Broegger has suggested, exactly as they do in a crystallizing beaker in the laboratory.* This appears to have been in part the molecule that formed the large placioclase ($Ab_1 An_1$). This has a temperature of fusion (1419° C) higher

* Exactly as Harker describes, loc. cit. p. 318.

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than nephelite or augite and thus can easily crystallize out if present in excess. Now of course in the feldspar series there is quite a range between $CaAlSi_2O_8$ and $NaAlSi_3O_8$ and just what may crystallize out must be a matter of pretty delicate balance in a many component system. But a lot of natural and artificial observations seem to indicate that in a dry igneous fusion the soda lime feldspars strongly tend to crystallize first, the residue containing more lime. This is characteristic of the diabasic texture, but in complex magmas the process seems to stop when the feldspar is as basic as augite. Augite, which can take in a little sodium and aluminum, as well as calcium, magnesium and iron, and indeed, almost every element present, may easily be last to form.

If then, in this zone of slow cooling the rock was for a long time below the fusion point of the plagioclase, but above that of the augite, say near 1200° centigrade, and if there was but little "juice" to keep the feldspars in solution and that being slowly lost, then if I read the facts aright, the feldspars aggregated in the cooler parts exactly like crystals on the walls of a beaker, and a more fusible augitic remnant collected toward the centre. Of course, too, the magma must be more alkaline than the eutectic.

The Mount Johnson plutonic was then, I should infer, formed under such conditions that:

1. M (the juice or mineralizers) were more promptly lost than T (the temperature), due either to connection with surface or dry environing rocks.

2. The cooling was very slow through the range of labradorite formation near the margin except directly at it. Thus 1200° centigrade was probably more than half the initial excess of temperature of the magma over the surrounding rocks. These are metamorphosed only near the neck and were probably at a temperature of less than 100° centigrade. The magma may plausibly have been not hotter than 2000° centigrade, yet a good deal above 1000° centigrade. Thus the grain and high temperature indicated, as well as the lack of recrystallization of the contact zone confirms the suggestion already made by Adams, that this is a volcanic neck or diatreme.

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THE HAYSTACK.

Now in the same way the Haystack* seems to have been highly superfused. The zone of finer grain (A and C) appears to be relatively narrow. After this formed, as the zone of slow cooling was crystallizing there was some disturbance and mixing, producing porphyritic dikes (B). At the same time there was a differentiation of (D, E and F) the more fusible parts, that is the more augitic, to the centre. This seems to be brought out nicely by comparing analyses with those of Mount Johnson.

COMPARISON OF ANALYSES.

Analysis VII (loc. cit. 1903, p. 271) of Mount Johnson, and C of the Haystack match, and I should interpret them as representing the primal magma cooled too quickly for differentiation.

Analysis VI represents the coarse grained transition, compare B.

Analyses I and II (1903, p. 265) represent the last crystallization, the most fusible augitic magma, and the likeness to D of the Haystack and their approximation to Bunsen's normal basaltic magma is striking. The most striking features are the rise in lime and drop in silica and alkalies.

Apatite, phosphorus and chlorine increase in the last crystallized part.

These then seem to represent the same kind of differentiation which I have found common among the Keweenawan surface flows.† It is interesting to find it here among the deep seated rocks.

This is quite different from a probably more common type of splitting in the plutonic rocks, shown in the quartz diabases,‡ which is proportional to the amount of juice that does not escape. A certain amount of the silica and feldspar substance

* Journal of Geology, 1906, p. 202.

† Magmatic differentiation in the rocks of the Copper-bearing series, Bull. Geol. Soc. Am. 1898, 10, p. 17.

‡ Compare the work of Lawson and myself, as well as the classic work of Teall and Vogt above cited.

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COMPARATIVE TABLE OF HAYSTACK AND MOUNT JOHNSON ANALYSES.*

	Margin, quickly cooled undifferentiated		1903 p. 265	Central, augitic, fusible			Bunsen's Normal Basalt
	VII 1903 p. 271	C 1908 p. 211 (Haystack)	VI	I	II	D	
SiO_2	57.44	57.98	50.40	48.85	48.69	47.87	48.47
TiO_2	1.97	0.90	1.17	2.47	2.71	1.02	
Al_2O_3	19.43	17.01		19.38	17.91	16.34	30.16
Fe_2O_3	1.69	3.34	5.58	4.29	3.09	3.59	
FeO	2.70	3.34		4.94	6.41	7.17	
MnO	0.25	0.12	0.77	0.19	0.15	0.14	
MgO	1.16	2.74		2.00	3.06	7.80	6.89
CaO	2.66	7.35	6.77	7.98	7.30	10.33	11.87
BaO	not det.	9.06 0.02 SrO			0.08	0.03	
Na_2O	6.48	3.92	6.24	5.44	5.95	2.43	1.96
K_2O	4.28	2.02	2.56	1.91	2.56	0.92	0.65
P_2O_5	0.60	0.43	0.09	1.23	1.11	0.41	
SO_3	not det.	tr.			MO CoO .05	CO_2 0.44	
Cl	tr.			0.68	0.95	NO 0.02	
H_2O −	1.03	0.14				0.28	
H_2O +	1.03	0.49				1.25	
Sum	99.69	99.86					

* From Adams, F. D. and Emmons, Journal of Geology, 1903, p. 271, and 1908, p. 211.

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is kept thereby in solution until after the augite has crystallized and the temperature has dropped to a point (750° centigrade) where quartz can crystallize. In such aqueous or mineralized magma the feldspar formation, in part anyway, follows rather than precedes that of the augite, and near the margin there is a tendency for the femic constituents to aggregate, that is, the augite, the hornblende, the iron ores. Compare group D of my paper above cited, the Sudbury ore bodies and the complementary micropegmatite, also the diabases and their aplites of the Cobalt region.* I have recently visited the "Lermondose"† and take that to be a basic marginal magmatic differentiation streak about a hundred feet from the margin of a gabbro, where the differentiation is of the aqueous type.

The presence of considerable quantities of graphic quartz and feldspar in the Haystack, however, indicates that there was some "juice" in this magma and that the differentiation may not have been wholly thermal, but in places quite the contrary. This complexity in differentiation seems to be the reason it is hard to interpret. For after the differentiation toward augite at 1200° centigrade, a differentiation toward micropegmatite may have taken place at lower temperatures.

While this paper is being printed a number of interesting facts have been developed by Tyrell, Hore, and others regarding differentiation, and there have been observations as yet unpublished by F. E. Wright and Bowen, which we cannot discuss at present.

* Canadian Mining Institute, Bull. 8 (1909), pp. 95–106.
†Journal of Geology, 1908, p. 124.

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Grain of Mount Johnson: Section From Centre East.

		HORNBLENDE *in mm.*	FELDSPAR *in mm.*
1223		10—12×2	40×8 13×3
1193	small hornblendes in feldspar, arrangement parallel to hillslope	10—12×2	65×15
	margin zone feldspar up to 90 mm., mica up to 12 mm., the coarser folia parallel		60—90
1133	faint dark banding, more femic, not so porphyritic	3×2	20—30
1113		5—7×1	20×10
1013		5—7×2	20—25×8
953	less porphyritic appearance	5—8×1	15—20×2
843	still less porphyritic; finer apparently; near pump above upper quarry	5×1	22×5 6×1
733	hornblende more idiomorphic, fainter porphyritic appearance; cross cleft running N30E	5—12×3	20×5
673	darker, more hornblende in blotches	5×5	20×5
590	section along here much covered	similar	similar
480	younger band; section much covered	7×2	12×12 5×2
370	idiomorphic hornblende, and macroscopic augite	5—7×2	20×10 to 31
269		similar	similar
150	still porphyritic rock a little poikilitic	similar	similar
90	hornblende poikilitic, feldspar idiomorphic	12×8	20×18
	dark, porphyritic and ophitic with augite, biotite 5 mm. Near by is a faint coarse mottling 12 to 20 mm. of blue spots and reddish interstices.		
0 at triangulation station near top			

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MERISTIC HOMOLOGIES IN VERTEBRATES.*

By J. S. Kingsley.

One of the most difficult problems in vertebrate morphology is to explain the serial homologies between the different groups. In the lower segmented animals these difficulties, although they exist, are far more simple and are far more easily explained. Thus no one has any doubt that the tenth or the fifteenth somite of Homarus is the exact equivalent of the serially homologous somite of Cancer. Between the larger Arthropodan divisions the task of comparisons of somites is possibly not so easy yet all attempts at drawing homologies between, say, a hexapod, an arachnid and a crustacean, are based upon the assumption of exact serial equivalency. It is true that one author or another has at times suggested the possibility of intercalation or elision of a somite, but these have been mere suggestions and have usually been discarded in the discussions.

In the vertebrates this comparison is more complicated. We are forced to assume that the shoulder girdle and fore limb of the frog are the homologues of those of man, although their connections are with entirely different somites when serial position is taken into account. In the case of the pelvic arch the numerical disparity of the corresponding somites is even greater, but in either case the identity of structure of arch and limb is so great that doubt of homology is practically impossible. How then has it come about that say the twelfth somite of the Amphibian is not homologue of the twelfth but of more nearly the twentieth of man?

In Gegenbaur's hypothesis that the girdles are derived from branchial arches and that these have migrated backwards over the post-cranial somites we have a possible explanation of these problems of the relations of girdles to body segments. The backward migration has been arrested at different points in the various groups. But this explanation will not suffice for other cases, hence the probability that it is true for none.

*Reprinted from the American Naturalist, Vol. 41, pp. 103–107, 1907.

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In the frog, as in all Ichthyopsida, there are but ten cranial nerves, while in the mammals there are twelve. There is no doubt that as far back as the tenth the nerves are exactly homologous in Amphibia and in the mammals. Relations to brain and to points of distribution place this beyond question, but what shall be said of the mammalian eleventh and twelfth? Are both of these nerves from the post-cranial region which have been transferred to the skull? If so, does it not follow that the cranium in the higher vertebrates is not the exact equivalent of that in the lower and that the differences have been brought about by the transformation of cervical into occipital vertebræ? If this, in turn, be so, are the occipital bones of the frog homologous with those of the mammal? Or are the basi-, ex- and supra-occipitals of the one merely analogues of those of the other? Is Huxley's argument for the derivation of the mammals from the Amphibia because of the double occipital condyles in the two groups based upon analogies rather than on true homologies? Are the condyles in Amphibia and Mammals not homologous but rather homoplastic formations?

Carrying this matter further back in the body, how are we to explain that apparent shifting of the pelvis in such a form as Necturus as described by Bumpus, Parker and others? Are somites ten, twenty and the like exactly equivalent in the normal and aberrant forms? And has there been an actual shifting of the pelvic girdle from one somite to the next in some individual? Or has there been an actual intercalation of vertebræ, the one to which the ilium is attached being constantly the same morphologically if not serially? Or, lastly, have the limbs and their arches arisen from a continuous fin fold and has every somite which contributes to that fold the potentiality of limb formation with all that this implies?

To take another case. In Amphioxus there is a large number of gill slits, a number which is doubled during development by the formation of the 'tongue bar.' Right behind the last gill slit comes the entrance of the hepatic duct into the alimentary tract, there thus being no œsophagus nor stomach intervening between the pharynx and the liver. Is this to be explained by saying that in the vertebrates the posterior gill clefts of Amphioxus

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have closed and that the space which they occupy has become converted into stomach and œsophagus? In other words are these formations of the vertebrate tube the homologues of a part of the gill region of the acraniate?

Then, too, what are to be done with cases of increased numbers of gill slits; the Notidanids with six or seven, the Californian Bdellostoma with its variable number, and Amphioxus itself? This question is wholly apart from that which discusses the relations between metamerism and branchiomerism.

Numerous other similar questions will readily suggest themselves to all. There is no reason for enumerating them here. The problem is, how are they to be explained. Must we find a separate explanation for each or can we find some one principle which will account for all?

This article is to be regarded in the light of a suggestion rather than a full reply with demonstrations of validity. I have no proof, other than analogies and the fact that the hypothesis here presented answers all the demands of the problem, that the explanation here advanced is the true one. It must be tested and the tests are not easily made.

In the invertebrate segmented animals there is, at the beginning, no metamerism. It appears later during growth, and in numbers of forms it is found that the segmenting tissues are produced by budding from groups of cells at the posterior end of the embryo. These are most familiar in the annelid teloblasts and are scarcely less well known in the Insects and Crustacea. Their number varies between wide limits, but for the present purposes the most important points concerning them, aside from their budding capacities, are their position in a more or less plainly marked transverse band and their situation at the extreme posterior limit of the growing embryo. Extensive examination of the literature has not shown similar budding cells in the Cuvierian group of Articulata in other places than the tip of the growing embryo, with the exceptions noted below.

It follows then that in these teloblasts and their equivalents are the full potentialities of the future somites. From them arise all the cells which are utilized in every structure which is metamerically repeated, the material for the new somite not being

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budded from any pre-existing somite, but always just in front of the hinder end of the body.

This applies strictly to all cases which are known to me in the arthropods as well as to most of the annelids; but in a few of the latter group modifications occur in the process which have great interest for us. As is well known, in a number of annelids asexual reproduction by transverse division occurs. At one or more points in the body a new head may develop, with the eyes, appendages, etc., characteristic of the anterior end of the worm, these features arising from a somite which in its earlier stages is apparently normal and like its fellows on either side. Then, just in front of this new head the worm divides and two worms, each with fewer somites than the original one, are produced and from this time onward lead an independent existence.

Of these only the anterior worm need now be considered. After the separation the segment which was just in front of the new head of course becomes the terminal somite of the new worm. The worm now increases in length and the new somites are formed by material cut off from the terminal somite which thus must have within it the equivalent of the teloblasts of the embryo.

From these facts it seems logically to follow that at least certain somites in the body have the potentialities of forming material for additional somites and must contain within them the same physiological possibilities as the original teloblasts from which they arise. In other words, in the annelid, before the beginning of the transverse division, the capacity for producing new tissues was located at more than one point in the body, but it was not exercised until after the asexual reproduction was well advanced.

In the case of the Naides the somites thus produced are all similar in character but in such instances as Protula, where heteronomous somites occur, the division of the worm is accompanied by the formation of new somites which differ in kind.

The application of these facts to the various types of meristic variation which occur in annelids need not be discussed here, but I think it is apparent that they will in part explain some of them. I do not mean to say that they reveal first causes but

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they do point out the mechanism involved and may be used to reduce all to a common rule.

In the same way the assumption that there are similar budding zones at various points in the vertebrate body will explain the various conditions outlined in the statement of the problem. In the vertebrates there is a continuous addition of new somites at the posterior end of the body as in the arthropods and annelids, implying the existence of the equivalent of teloblasts at the posterior end. The assumption of budding zones at other points will explain the other features noted. Such a zone in the occipital region will allow us to explain the difference in the number of cranial nerves in the mammals and in the Ichthyopsida and yet allow us to accept the homology of the occipital bones throughout the vertebrate series. The additional nerves are thus to be regarded not as transferred from the neck but as new or intercalated structures. In the same way we may explain the varying number of vertebræ in the different regions and allow at least one of the pelvic vertebræ to be regarded as a fixed point and we may be relieved of any assumption of a shifting of the girdles. It will also explain many anomalies such as the attachment of the two halves of the pelvis to different vertebræ and the increased number of lumbar or thoracic vertebræ in man.

This is to be regarded solely as an hypothesis. So far as I am aware no one has seen such budding zones in any vertebrate. In fact it is extremely probable that there is no such well defined zone as is found in the band of teloblasts of the crustacean. It is to be regarded rather as a series of assumptions, based in part upon analogies, which, if true, would explain the questions with which the present note began. The hypothesis is presented as a suggestion to stimulate investigation and criticism upon an interesting and difficult subject.

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AN UNATTACHED ZOOSPORIC FORM OF COLEOCHÆTE.

By F. D. Lambert.

The material on which this paper is based was found growing in the gelatinous substance surrounding frogs' eggs which were developing in a laboratory aquarium at Tufts College. The eggs, collected from a small pond in the Middlesex Fells, Medford, Massachusetts, early in May, 1909, were already in an advanced stage of development and the mass showed a characteristic green color. This was due to the presence of certain unicellular algæ, familiar to me by reason of several seasons' observations. Growing with these algæ were numerous specimens of a setiferous form which I had not seen before. Almost all the specimens of this alga were discs, monostromatic except in one place, usually the centre, where an upper cell invariably bore a very long and extremely delicate articulate hair, sheathed at its base. Hairs of the same type were frequently borne by other cells of the disc, only one surface of which was setiferous. As the angle of insertion was not constant, the hairs pointed in all directions. The basal sheaths were often so inclined that the hairs extended in a plane parallel to that of the disc. Hairs of the marginal cells of the discs sometimes extended radially. The smallest specimens observed had but two cells, of which the upper, smaller cell bore the sheathed and jointed hair. In some specimens the disc was more than one cell thick in regions other than the centre, and in a few of the plants observed, certain areas of the disc were at least three cells thick. While some of the discs were symmetrical and regular in their marginal outline and perfectly flat, others were irregular in outline and arched. For specimens of the latter type, the term disc seems a misnomer. All of the cells were uninucleate, with a single, light green, definitely outlined chromatophore, which in most cases extended over the greater part of the cell wall and contained a single large and conspicuous pyrenoid. That the plants were in a mature reproductive condition was evident by

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the presence, in a majority of specimens irrespective of size, of certain empty cells which had functioned as sporangia and each of which had a single round opening in its wall. As it was thought the alga might prove of interest, a large number of the plants were studied and measured, and camera drawings were made of approximately forty specimens.

Reference to the general literature of the chætophoraceous Chlorophyceæ showed that several of my figures of the smaller, earlier stages very closely resembled Oltmanns' (1904) copies of Pringsheim's (1860) figures of the early stages of *Coleochæte scutata*. In Pringsheim's classic account of this species these figures, together with several others Oltmanns did not use, were intended to serve two purposes, viz., to illustrate (1) the early development of the sexual plant, and (2) the development of an asexual plant. This asexual plant had been recognized and especially emphasized by Pringsheim. According to Pringsheim's account of Coleochæte, the asexual plant, arising from the germinated oospore, gives rise to zoospores. These zoospores germinate to produce small plants which are propagated exclusively by zoospores, ". . . erzeugen keimend nur solche Pflanzen, die sich ausschliesslich durch Schwärmsporen vermehren." (p. 25.) After a number of generations, "Erst nach einer je nach der Art verschieden langen Reihe von Generationen ungeschlechtlicher Individuen . . ." (p. 25) these small asexual plants produce zoospores which give rise to the larger thallus. This latter thallus, after a period of zoosporic reproduction, finally develops the sexual organs. It seems strange, however, that although Pringsheim lays stress upon the existence of these dwarf zoosporic plants, he does not refer to them in that part of his text which embodies the discussion of his figures, or in the description of his plates. It is evident, however, that three of his figures, *b*, *c*, and *e*, Plate II, no one of which has been used by Oltmanns, can be interpreted as illustrations not only of the dwarf zoosporic plants but also of stages in the development of the sexual thallus. The argument for such an interpretation is based upon the following evidence. Pringsheim, in his figures *a*, *g*, *d*, and *h*, Plate II (used by Oltmanns), represented the cells of the thallus as containing protoplasmic structures. In some of these figures the chromato-

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phore is clearly distinguishable. In figure *g*, Plate II, the large chromatophore of each of the three disc cells contains a body which might be safely interpreted as a pyrenoid. In his figures *b*, *c*, and *e*, Plate II (omitted by Oltmanns) all cells are represented as devoid of contents. It is very significant, however, that in each of these plants, *b*, *c*, and *e*, Plate II, every cell, with the exception of the single, dorsal, setiferous cell, shows a circular or ovoid structure which I interpret as an opening for the liberation of a zoospore. That these circular or ovoid structures cannot be interpreted as pyrenoids, is shown by their absence not only in all the dorsal setiferous cells, which never produce zoospores, but also in the cells which contain the chromatophores and pyrenoids previously mentioned.

In his discussion of the generic characters of Coleochæte, Pringsheim calls attention to the jointed hairs, ". . . lange, äusserst dünne, hohle cylindrische Fäden, die in ungefähr gleichweiten Strecken zellenartig abgegliedert erscheinen" (p. 12), which are shown in two figures of *Coleochæte soluta*, 1*m*, 2*m*, Plate IV, and in two of *Coleochæte pulvinata*, 1*m*, 14*m*, Plate V. That he did not regard the septate hairs as multicellular structures, however, is clearly evident by his statement: "Ich zweifle jedoch dran, dass es wahre zellige Fäden sind" (p. 12), . . .

Brébisson (1844) in the original description of Coleochæte, described the hairs as sheathed at the base, but failed to note the articulation, and in his figures the hairs are represented very simply by single lines. He also failed to observe the dwarf zoosporic plants.

The articulation of the sheathed hairs, described by Pringsheim, has not been recognized by Jost (1895), Oltmanns, Chodat (1898), West (1904), Collins (1909), or Wille (1897). It is of interest to note, however, that Wille illustrates the articulation of the hairs in the figures which he copied from Pringsheim.

The dwarf plants, described by Pringsheim, which reproduce exclusively by zoospores were not recognized by Jost. In his account of the Coleochætaceæ, which includes a brief discussion of alternation of generations of Coleochæte, Wille mentions

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but does not figure the dwarf zoosporic plants, "zwischen gewöhnlichen Individuen und den bei der Keimung der Schwärmspore enstandenen Zwergescheiben." Oltmanns' unwillingness to recognize the existence of the dwarf zoosporic plants of Coleochæte is evident in his statement: "Niemals aber sicht mann, dass irgend ein Polster nach die zoosporenbildung ze grund ging, wie Pringsheim anzunehmen scheint," . . . (p. 12). In his later treatise (to which I have referred above) although he states that the Coleochæte plants, which in spring develop from the oospores, give rise to new plants, he does not regard these generations as exclusively zoosporic. None of Chodat's figures, illustrating several stages in the germination of the zoospores of *Coleochæte pulvinata*, resemble any of the plants which I have observed. One figure of a small plant shows one cell which has functioned as a sporangium. As he did not discuss this plant, he probably considered it merely a young stage in the development of the sexual thallus. In his opinion no stage in the development of Coleochæte is exclusively zoosporic. In discussing the life cycle of Coleochæte, West says, "The zoospores of Coleochæte give rise to several rudimentary asexual generations which are propagated by zoospores and finally to a sexual individual." Collins, in his discussion of Coleochæte, does not mention the rudimentary zoosporic plants.

Fig. 12 illustrates a two-celled plant which resembles very closely Pringsheim's figure of the two celled stage of *Coleochæte scutata*. The germinating zoospore has divided horizontally into a dorsal, "obere," and a ventral, "untere," cell. The characteristic hair, sheathed at the base and jointed, arises vertically from or near the middle of the upper surface of the dorsal cell. The dorsal cell does not divide. The disc of the thallus is developed from the ventral cell. In fig. 10 the ventral cell has divided by a vertical wall into two cells of approximately equal size. Two- and three-celled plants of this type are very common. Occasionally, as illustrated in fig. 14, the ventral cell divides obliquely. The two ventral cells of the disc are next divided by another vertical wall, at right angles to the first, thus giving rise to a plant consisting of a four-celled disc

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surmounted by a single setiferous cell (fig. 15). Such symmetrical specimens are very common. The first vertical division of the ventral cell usually results in the formation of two daughter cells of unequal size, the larger of which then divides in a plane parallel to the first vertical wall. The disc of such a plant consists of three cells, one median and two lateral (figs. 8 and 11). The median cell of the disc next divides in a vertical plane at right angles to the first two vertical walls (fig. 17). From this point onwards, radial and tangential divisions of these cells alternate with considerable regularity, the tangential divisions cutting off cells from the bases or inner ends. Internal cells thus cut off do not divide again, and all increase in the size of the disc results from division of the peripheral cells. (See figs. 21, 2, 3 and 4.) This manner of development differs in no respect from that described by Pringsheim. While there is no difficulty in recognizing the successive planes of cleavage in discs of the smaller symmetrical specimens, the interpretation of the order of formation of such planes in the larger and older specimens is usually extremely difficult. This difficulty is due to the fact that in specimens of the latter type the outline of the disc is often deeply notched and otherwise irregular. See figs. 1 and 7.

According to Pringsheim's account, the discs of *Coleochæte scutata* are always uniformly monostromatic. A few specimens which I have studied have shown disc cells divided horizontally. The disc cells are usually rounded ventrally, and this feature is so marked in many of the smaller specimens, that the disc cells, varying in dorsoventral diameter, appear to be separated ventrally. See figs. 8, 11 and 13. Some of the larger specimens show a distinct dorsal arching of the disc, the middle cells of the disc being elevated somewhat above the cells of the periphery as in fig. 16. This peculiarity may be due to the fact that the discs occur in a homogeneous gelatinous medium in which they develop without a subtratum. Fig. 6 represents a plant in which the absence of a subtratum has made it possible for a zoospore to escape through a hole in the ventral side of a disc cell. The smallest specimen which showed sporangia (fig. 19), had a disc of four cells, each of which was empty and had an

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opening through which a zoospore had undoubtedly escaped. The fact that the four sporangia constituted the entire disc proved conclusively not only that this plant was mature, but also that the production of its zoospores ended its existence. One disc of two cells (fig. 14) had a protuberance which suggested an incipient zoosporic aperture. However, the untimely death of this specimen prevented further observations as to the nature of the papilla. The presence of sporangia in the periphery of several larger specimens demonstrated not only their maturity, but also the end of their existence. The zoospores develop one in a cell in the manner described by Pringsheim. Although various stages in the development of the zoospores were observed, I did not see the motile zoospore. When the cell wall gives way for the liberation of the zoospore, the edges of the wall surrounding the opening project outward in such manner that a side view suggests a tubular aperture, fig. 6, 16, 19, 9, 21 and 22.

The hairs, always borne by the original dorsal cell and sometimes by other cells, are essentially like those described by Pringsheim. The consecutive segments of one of these hairs, selected at random, measured as follows: 16, 67, 40, 67, 57, 43, 33, 53, 57, 78, and 66 microns. Many hairs were more than 4.5mm. long These long hairs, although extremely delicate, could be traced very distinctly and without difficulty throughout their course in the gelatinous medium. Many of the longer hairs of single specimens and sometimes those of adjacent specimens were tied in large loose knots.

The smallest specimen of the dwarf zoosporic plant observed measured 23×30 microns (fig. 12); the largest, 57×106 microns.

One specimen observed (fig. 22) was very different from all the others. As it was not of the discoid type, a single, dorsal, setiferous cell, comparable to the dorsal setiferous cell of *Coleochæte scutata*, could not be recognized. Many of the cells had developed into sporangia. Whether this is merely an aberrant form of *Coleochæte scutata* or a dwarf zoosporic plant of some other species of Coleochæte, it is impossible to determine.

If, as seems to be the case, the small plants described and figured in this paper are the dwarf zoosporic plants of *Coleochæte*

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scutata, this contribution confirms Pringsheim's account of Colechæte, in which the dwarf plants, exclusively zoosporic, were described and emphasized as an independent phase in the life history.

Since the consideration of Coleochæte as the ancestor of the Bryophytes is based on the interpretation of its fructification, which is the highest type in the green algæ, there may be some interest attached to the dwarf zoosporic plants which appear as an independent phase in the life history of the genus.

Coleochæte offers a particularly interesting and promising field for cytological investigation. This is especially true with respect to the chromosomes, inasmuch as such an investigation will lead to a true interpretation of the gametophytic and sporophytic phases of the life cycle, and thus will show definitely the position of the dwarf zoosporic plants in the alternation of generations.

LITERATURE CITED.

1844 Brébisson, A. de. Description de deux nouveaux genres d'Algues fluviatiles. Ann. d. sci. nat. III, 1, Botan., Paris, 1844.

1860 Pringsheim, N. Beiträge zur Morphologie und Systematik der Algen, III, Die Coleochæten. Prings. Jahrb. f. wiss. Bot. 2, 1860.

1895 Jost, L. Beiträge zur Kenntniss der Coleochæten. Ber. d. d. bot. Ges., 13, 1895.

1897 Wille, N. Coleochætaceæ in Engler and Prantl, die Nat. Pflanzenfamilien, Th. I, Abl. 2, 1897.

1898 Oltmanns, Fr. Die Entwickelung der Sexualorgane bei Coleochæte pulvinata. Flora, 85, 1798.

1898 Chodat, R. Études de biologie lacustre. Coleochæte pulvinata. Bull. de l'Herb. Boiss., 6, 1898.

1904 Oltmanns, Fr. Morphologie und Biologie der Algen. I, Jena, 1904.

1904 West, G. S. The British Freshwater Algæ. Cambridge, 1904.

1909 Collins, F. S. The green Algæ of North America. Tufts College Studies, 2, 1909.

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EXPLANATION OF PLATE.

All figures × 600.

Fig. 1, 2. Ventral view of plant with asymmetric disc.

Fig. 3, 4. Ventral view of plant with symmetrical disc, cells divided by radial and tangential walls.

Fig. 5. Lateral view of plant of four cells, dorsal cell setiferous, disc of three cells; right side of disc two cells thick, upper cell bearing seta.

Fig. 6. Lateral view of plant with disc three cells thick, four of the disc cells zoosporangia.

Fig. 7. Ventral view of asymmetric disc, deeply notched on one side.

Fig. 8. Lateral view of plant with disc of three cells.

Fig. 9. Plant with three zoosporangia in periphery of disc.

Fig. 10. Lateral view of plant with disc of two cells.

Fig. 11. Lateral view of plant with disc of three cells.

Fig. 12. Lateral view of plant with disc of one cell; *c*, chromatophore; *p*, pyrenoid; *s*, septum in seta.

Fig. 13. Lateral view of plant with four-celled disc.

Fig. 14. Lateral view of plant with disc of two cells, vertical wall separating disc cells somewhat oblique, papilla developed on one side of one of the disc cells.

Fig. 15. Ventral view of plant with disc of four cells.

Fig. 16. Ventral view of plant with arched disc, cells in middle of disc not visible when those at the periphery are in focus, three zoosporangia in periphery of disc.

Fig. 17. Dorsal view of plant with disc of four cells.

Fig. 18. Lateral view of plant with one of the disc cells divided horizontally.

Fig. 19. Lateral view of plant in which all of the disc cells have functioned as zoosporangia.

Fig. 20. Plant with disc of four cells, one disc cell setiferous.

Fig. 21. Plant with disc of five cells, one of which has functioned as a zoosporangium.

Fig. 22. Plant of very irregular type, three zoosporangia, setæ on all sides.

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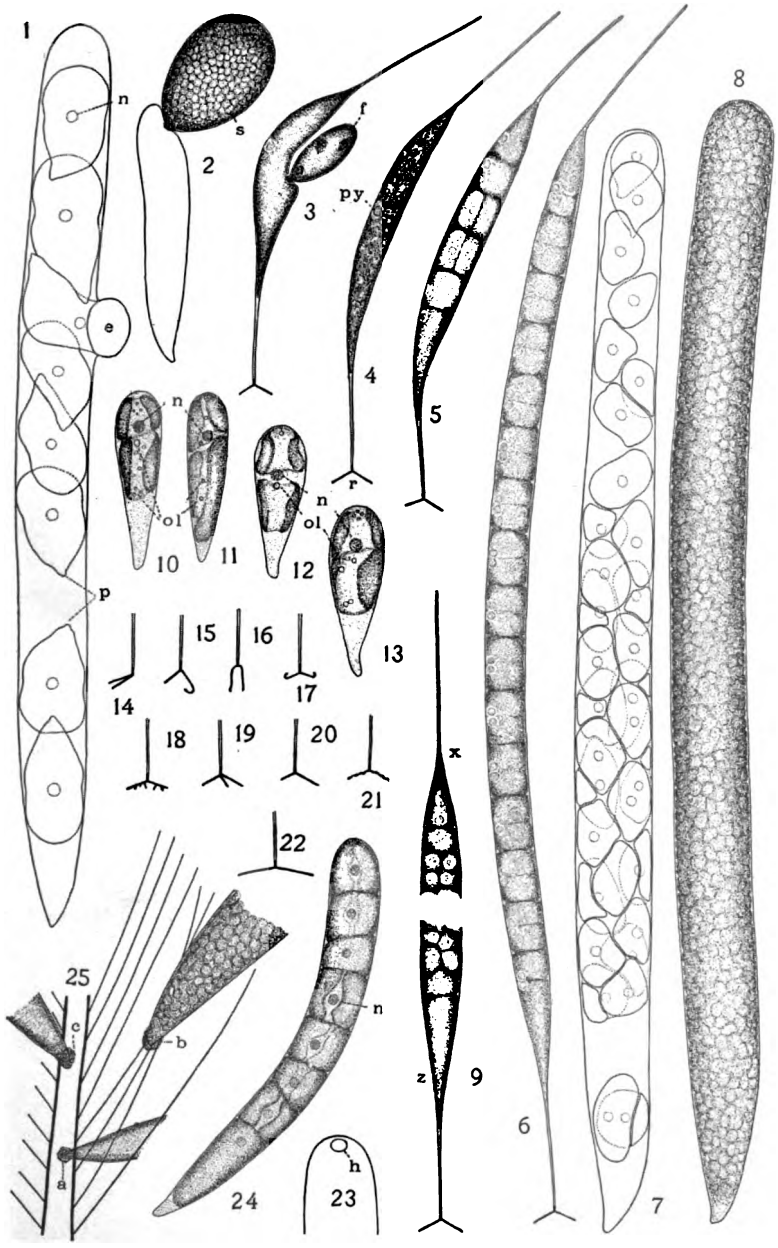

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NEW SPECIES OF CHARACIUM

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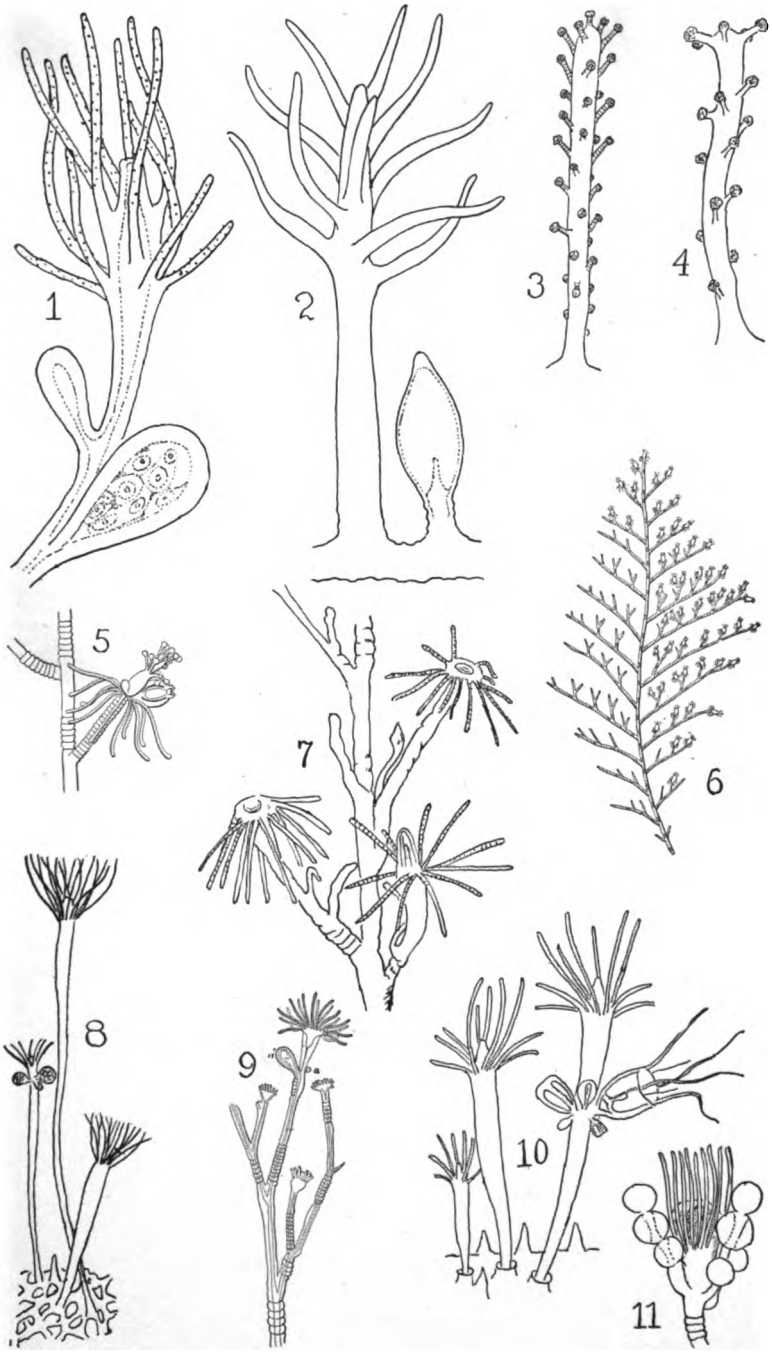

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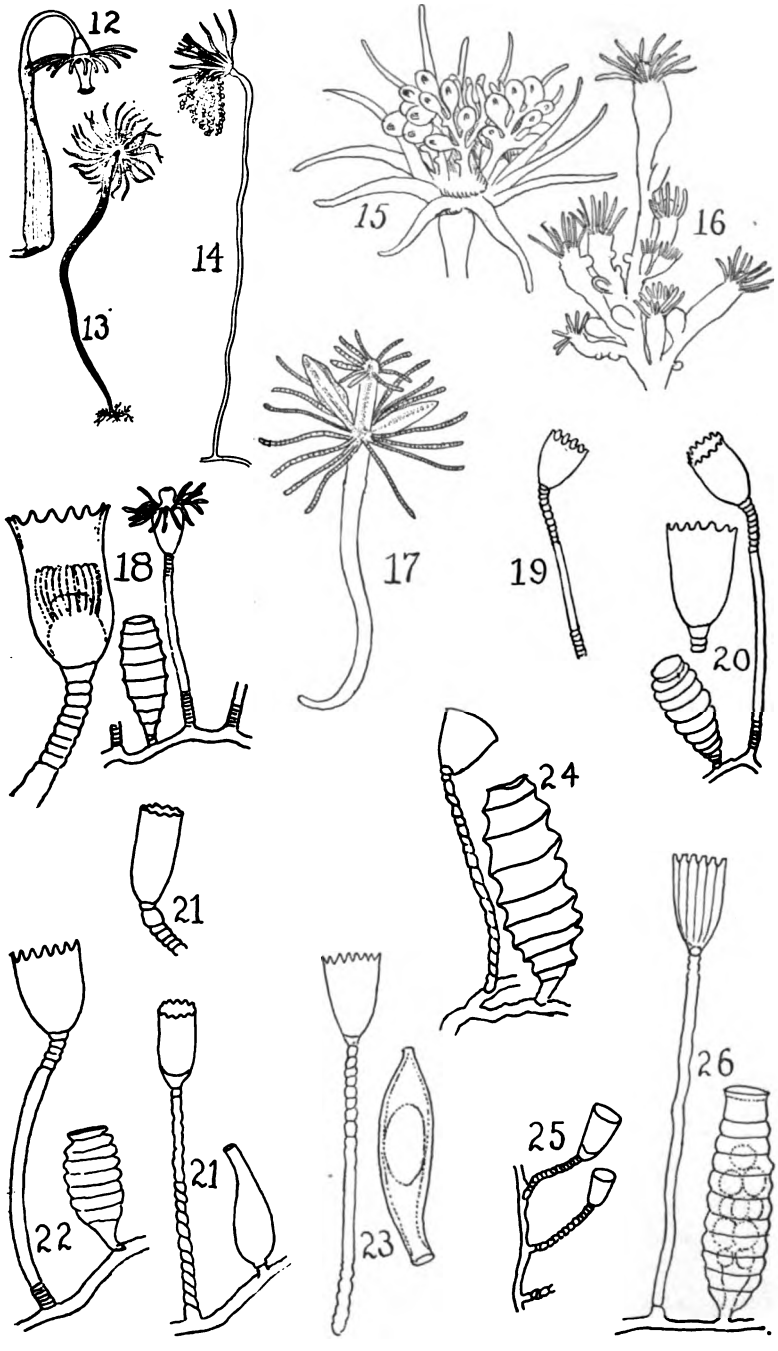

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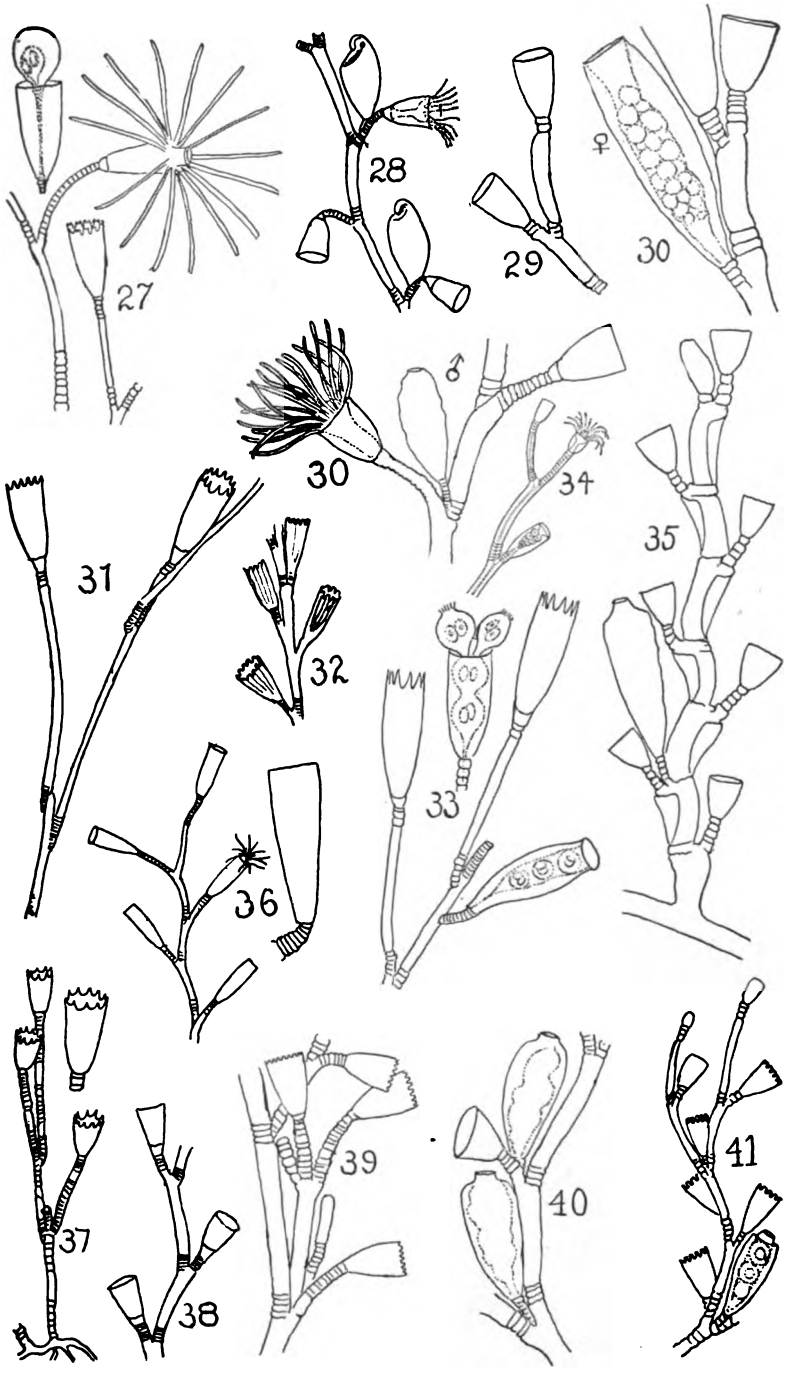

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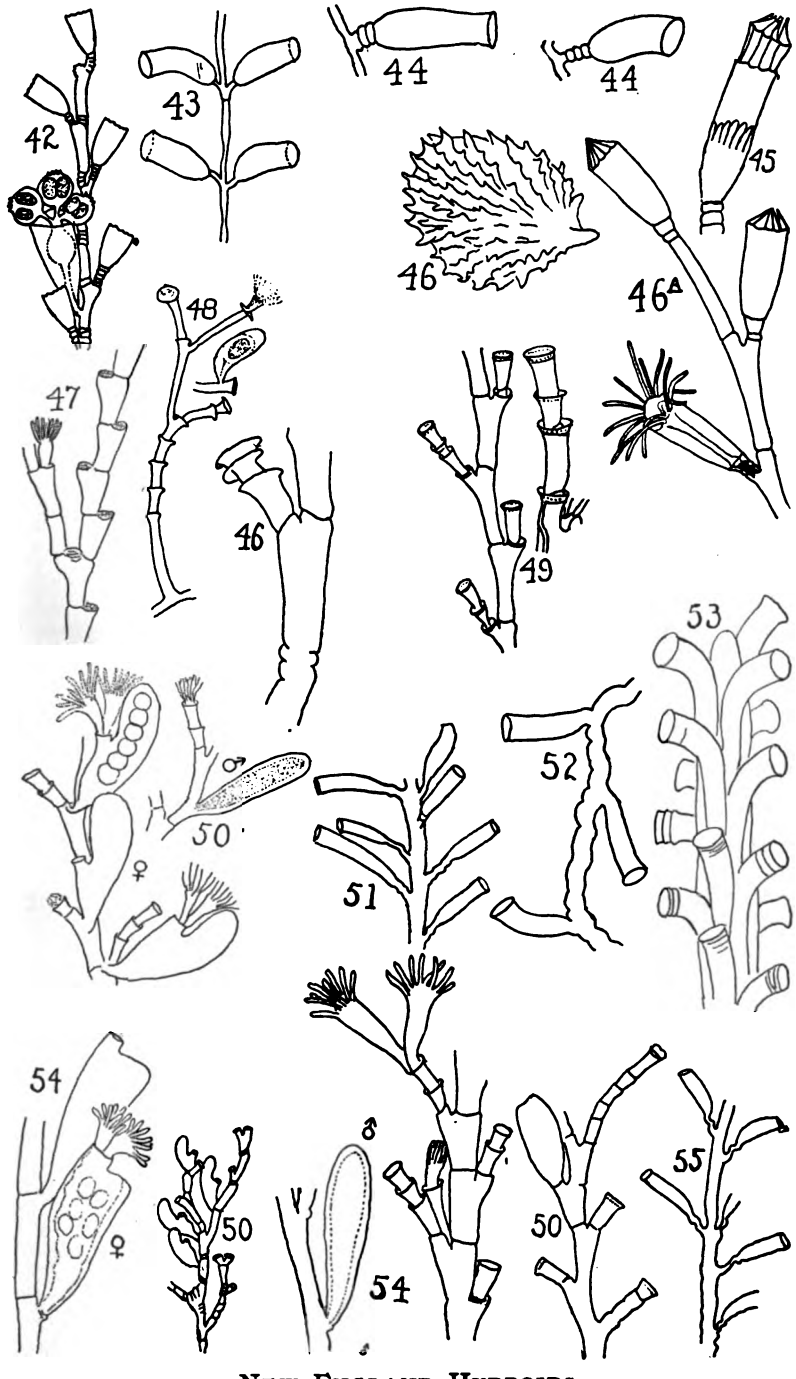

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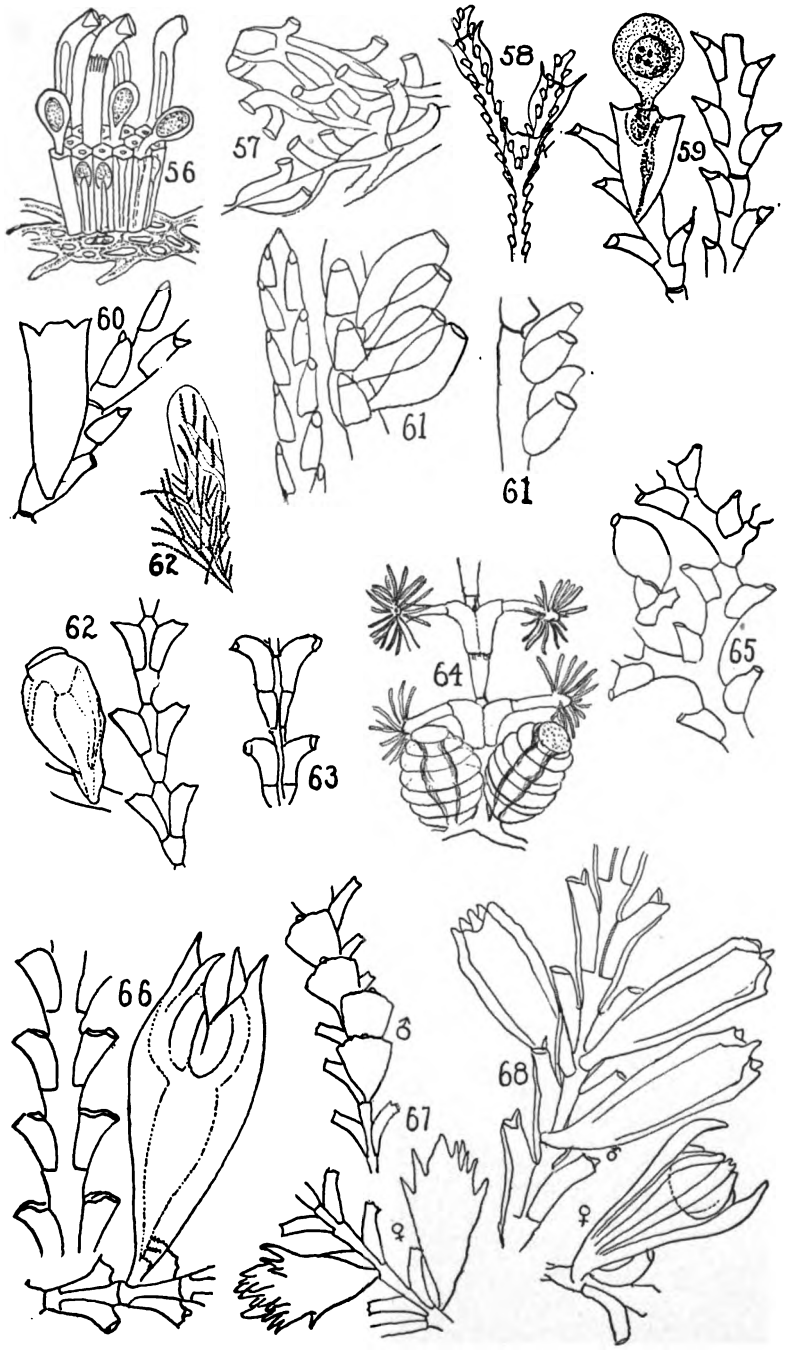

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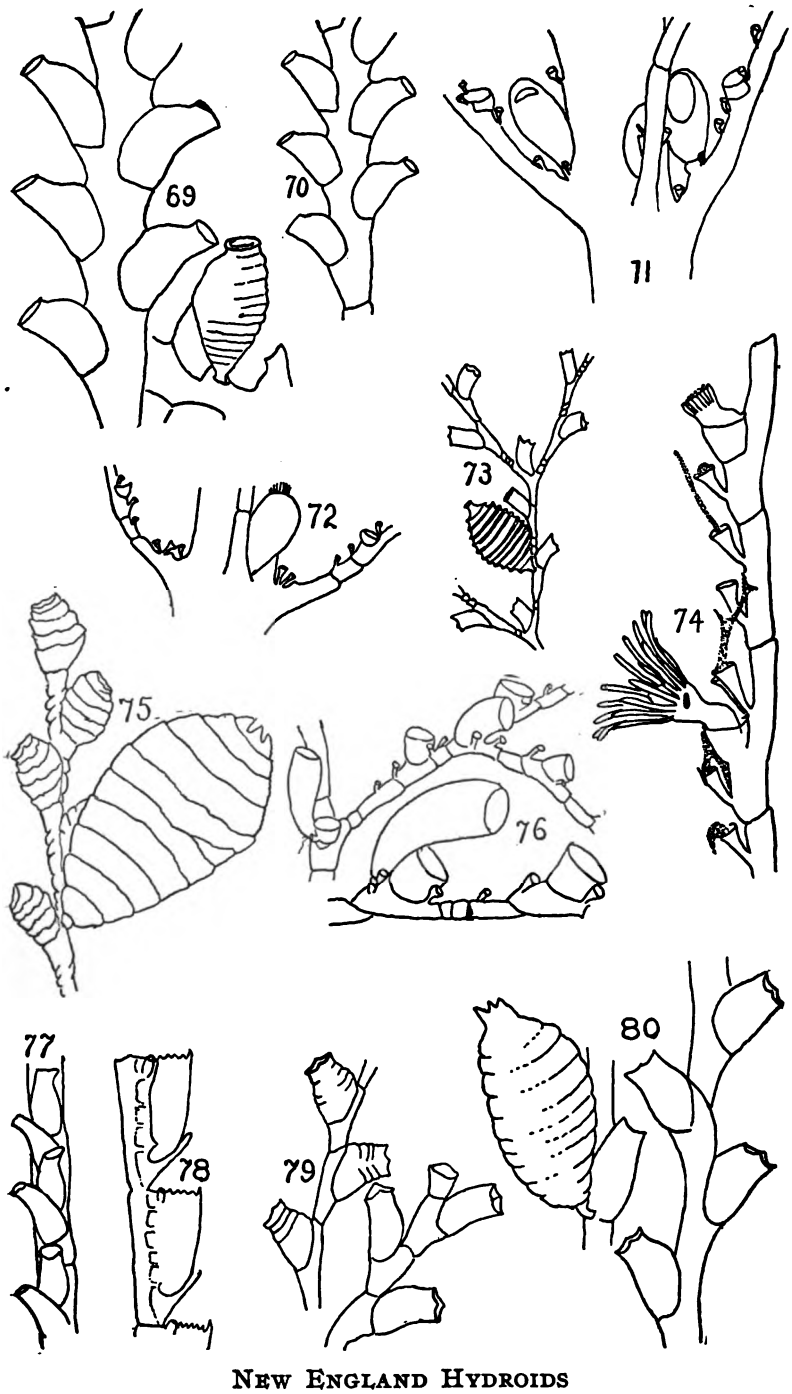

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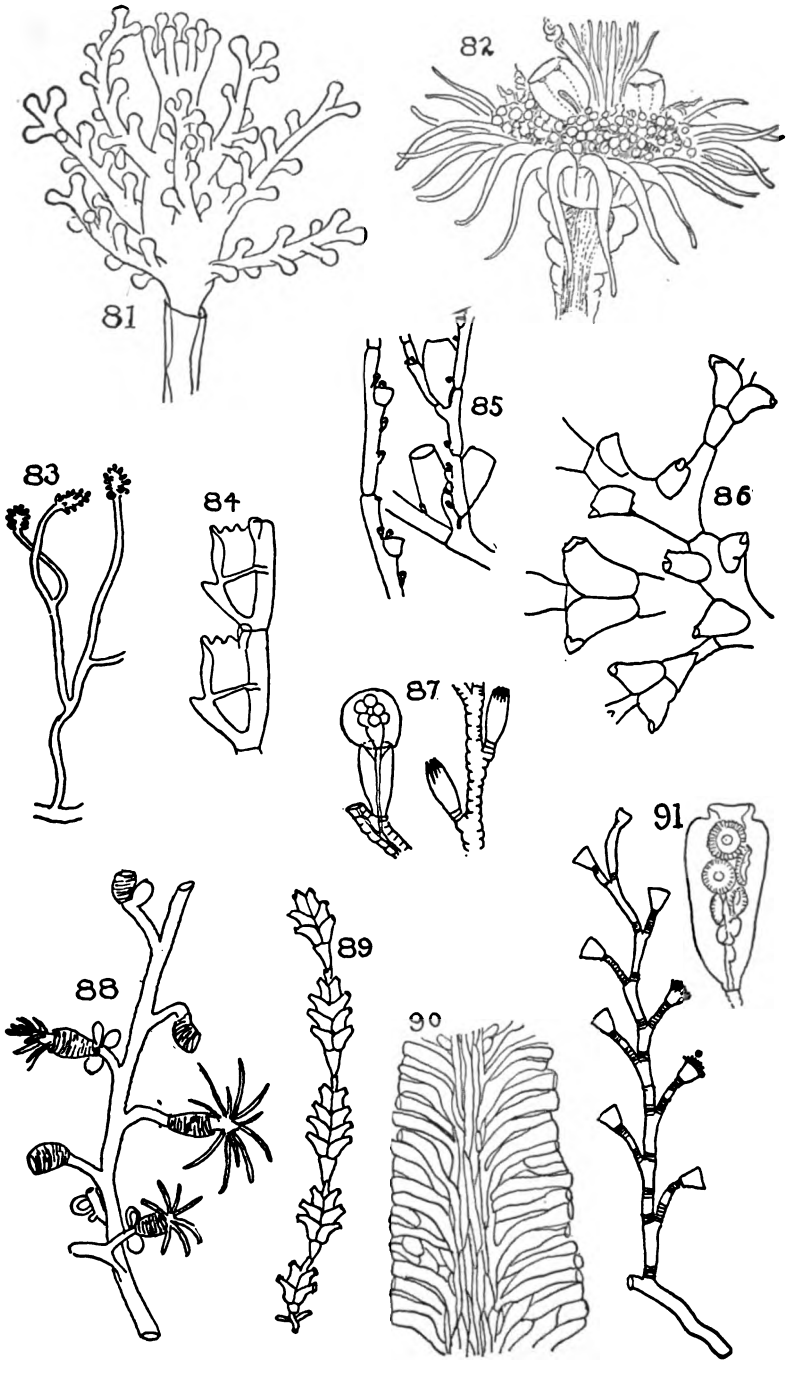

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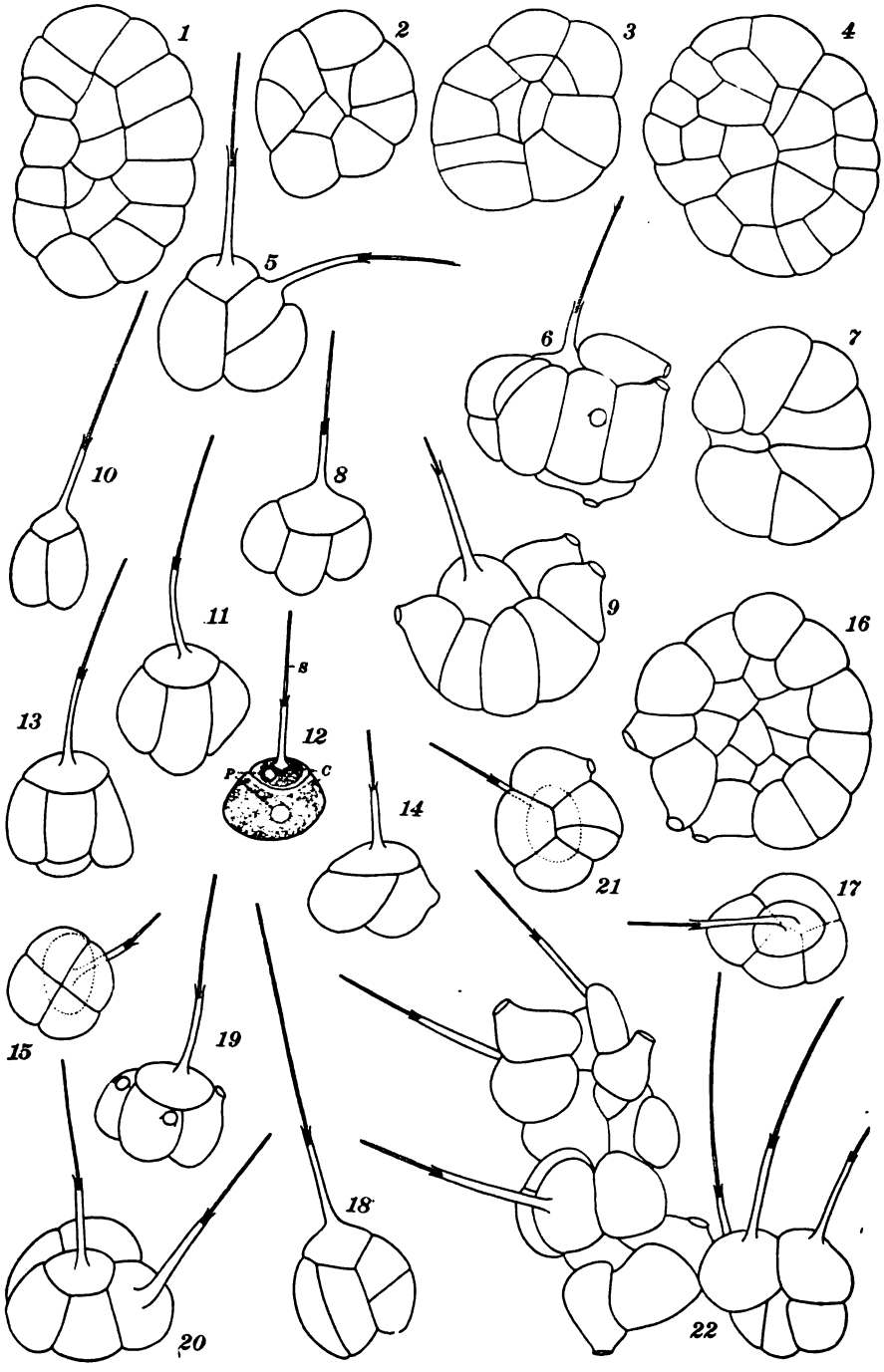

AN UNATTACHED ZOOSPORIC FORM OF COLEOCHÆTE

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TUFTS COLLEGE STUDIES, Vol. III, No. 2.

(SCIENTIFIC SERIES.)

THE GREEN ALGAE OF NORTH AMERICA,
(SUPPLEMENTARY PAPER.) By FRANK S. COLLINS.

DIDYMOSPORANGIUM REPENS,
NEW GENUS AND SPECIES OF CHAETOPHORACEAE.
By F. D. LAMBERT.

PUBLISHED BY THE CHARLES HYDE OLMSTEAD FUND.

TUFTS COLLEGE, MASS.
APRIL, 1912.

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TUFTS COLLEGE STUDIES, Vol. III, No. 2.

THE GREEN ALGAE OF NORTH AMERICA, SUPPLEMENTARY PAPER.

By Frank S. Collins.

In the paper by the writer on the Green Algae of North America, Vol. II, No. 3, of these Studies, the hope was expressed that it might be of use in encouraging further investigation and study. It is a satisfaction to record that this hope has been realized; from all over the country reports of new localities have been received, increasing the known area of distribution of many species; and names and descriptions of a not inconsiderable number of species not before known in North America will be found in the following pages. Among the printed papers from which these additions have been taken, is Hayden, 1910, a study of the algae found in the Missouri Botanical Garden, adding several species; Börgesen, 1911, adds to our knowledge of the West Indies, and gives us some new species; in his paper a considerable number of changes have been made from specific to varietal rank, etc., but such matters are largely a question of individual opinion, and we have not gone into the details here. Gepp, 1911, though nominally referring to the results of the Siboga Expedition, is really a monograph of the Codiaceae, covers many of the species of our region, and adds some new forms.

The most important general work on the green algae is Wille, 1909; in this will be found a resumé of all that has been done in this field from 1897. The publication of new genera has gone on during that time at a rapid rate, and a collection in compact shape of descriptions and references, with a critical study of their validity by such an authority as Wille, is of the utmost value. The mortality among these new genera under his treatment has been great, and while some students may not agree with his decision in every case, everyone will find the work useful. Wille's work was in press at the time the paper on the

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green algae of North America came out, so that the latter did not have the advantage of Wille's work; which, on the other hand, was so far advanced that it could not refer to the American paper. Wille has made numerous changes in classification, but as it is not likely that his present arrangement is final, any more than its predecessors, and as the work is easily obtainable, no attempt has been made to revise the American paper in conformity. A list of all the works cited in this supplement which were not in the similar list in the original will be found at the end of the paper.

The form chosen for the present paper is somewhat like that of Wille, 1909, or like the Emendation of the seventh edition of Gray's Manual, by B. L. Robinson and M. L. Fernald, in Rhodora, Vol. XI, p. 33, 1909. This has been found a convenient way of presenting what is a matter of both addition and revision; everything is referred to the page in the original paper containing the matter requiring revision, or in case of new matter, where it would have been placed if available at the time of publication. The keys for the determination of genera, species, etc., have been found useful to students using the work; to continue this usefulness to as large an extent as possible, these keys have been extended to cover the additional genera and species; the student can insert these additions by interlining or marginally, and the key will then be complete, including everything in both the original and the supplementary papers. New localities have been given only when indicating a much more extensive range than before known; new stations of similar character to the older records have not been given. With each species originally described was given a reference to some issue in exsiccatae, if such there were; the same has been done with species now appearing for the first time; in fascicles XXXII to XXXVII of the Phycotheca Boreali-Americana, issued in the last three years, a number of species, described in the original paper, have been distributed for the first time in that series; instead of referring to each by page, an alphabetical list will be found at the end of this paper. To carry out the original plan, a figure is given for each genus in the present paper that was not figured in the original paper; figures have

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also been given for new species here published. Localities have been given in fuller detail than was possible in the original paper, where so many species had to be described in limited space, and the collector's name has here been added; where no name is given, the collection was made by the author.

Under the rules of the Vienna Congress of 1905, all publications of new genera, species, etc., must now be accompanied in each case by a Latin diagnosis, which rule has here been followed; a diagnosis in English has been added. The Brussels Congress of 1910 adopted full rules for the nomenclature of algae, with the exception of the list of nomina conservanda; the only change affecting the green algae is that Hirn, 1900, is taken as the basis for the nomenclature of the Oedogoniaceae, and names there used are not to be changed on account of any prior publication. Where a name is given by Hirn as from some earlier work, it is now to be cited in the form of "Wittrock, ex Hirn, 1900."

Page 102, Key to the Genera of Zygnemaceae, change to read,

1. Two cells uniting to form one before the formation of the spore. 2.
1. Each cell dividing; spore then formed by the union of the two secondary cells. 4. ZYGOGONIUM.
2. Color normally purple; chromatophores two, disk-shape. 4. PLEURODISCUS.
2. Color normally green. 3.
3. Chromatophores two, star-shaped. 1. ZYGNEMA.
3. Chromatophores one or more, parietal, more or less spiral. 2. SPIROGYRA.
3. Chromatophore an axial plate. 3. DEBARYA.

Page 104, before Z. STELLINUM, insert,

Forma **leiosporum** nova forma; P. B.-A., No. 1767. Sporae membrana mediana levi; cellulis fertilibus modice inflatis.

Median membrane of spore smooth; fertile cells somewhat swollen; otherwise as in the typical form. Lake Temescal, Cal., W. J. V. Osterhout. Type in herb. F. S. C., No. 571.

Page 107, for No. 34 of key, substitute,

34. Cells not over 35 μ diam. 35.
34. Cells 39-42 μ diam. 36. S. *insignis*.

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35. **Chromatophores 2; dissepiments uniformly replicate.**
35. *S. Hassallii.*

35. **Chromatophores 3; dissepiments frequently plane.**
37a. *S. inconstans.*

Page 106, for No. 17 of key, first line, substitute,

17. **Cells 21-40 μ diam.** 10. *S. decimina.*

Page 107, for No. 25 of key, second line, substitute,

25. **Cells 50-65 μ diam.** 23. *S. neglecta.*

Page 108, before S. JUERGENSII, insert,

Var. **tenuispira** nov. var.; P. B.-A., No. 1668. Chromatophora unica, tenui; filamentis 30μ diam.; sporis 60-65μ×32-35 μ.

One slender spiral chromatophore; filaments 30 μ diam.; spores 60-65×32-35 μ. Type from Lake Quannapowitt, Wakefield, Mass., July 18, 1909, in herb. F. S. C., No. 6065a. Also from Oberlin, Ohio, F. O. Grover.

S. porticalis is a common species with considerable range in its dimensions; the var. *tenuispira* has filaments of a diam. about at the lower limit of the typical form, and the spores are correspondingly narrow. It has been collected in Ohio as well at two stations in Mass., and the characters are quite uniform in all. The slender spiral in the place of the broad dentate spiral of the typical *S. porticalis* is noticeable. The plant may yet prove to be a good species.

Page 110, Var. SUBMARINA, change to read,

Filaments 21-32 μ diam.

and add note,

Material from a small pond, Nonamesset, Elizabeth Islands, Mass., Aug. 8, 1909, No. 6078, F. S. C., has filaments 21 μ diam., chromatophores usually 2, occasionally 3, rarely 1.

Page 112, before S. MAXIMA, add,

A form found in a swamp beside Willow Road, Reading, Mass., May 23, 1908, No. 5807, F. S. C., has fertile cells somewhat swollen, and chromatophores with numerous though rather small pyrenoids, in these respects approaching *S. bellis*, but on the whole nearer to *S. orthospira*. A form collected by E. N. Transeau at Charleston, Ill., also has swollen cells, about 50 μ diam. at the ends, 65 μ at the middle; chromatophores 5 or 6.

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Forma **purpurea** nova forma; P. B.-A., No. 1771. Colore saturate vel nigro-purpurea.

Color dark or blackish purple; forming thin sheets in a cranberry bog, Eastham, Mass., July 8, 1911. Type in herb. F.S.C., No. 6353. In this station the sheet remained moist, though the water had mostly fallen away from below it; the fruit was formed the same as in the normal form.

Page 114, for No. 23, substitute,

23. S. NEGLECTA (Hass.) Kützing, 1849, p. 441; Petit, 1880, p. 26, Pl.IX; figs 1-5; ? Wolle, 1887, p. 216, Pl. CXXXVI, figs. 8 and 9; *Zygnema neglectum* Hassall, 1845, p. 142, Pl. XXIII, figs. 1 and 2. Tilden, American Algae, No. 159. Filaments 50-65 μ diam., cells 2-5 diam. long; chromatophores 3, narrow, with apparent median line uniting the rather small and distant pyrenoids, making 1½-2 turns in the cell; fertile cells rather shorter and slightly swollen; spores ovoid, 50-60 μ diam., 1-1½ diam. long. Mass., Ill., Colorado. *Europe.*

From Wolle's comments it is doubtful if his plant, from South Carolina, belongs here, and there has been no other American record, except Miss Tilden's distribution, but it has recently been found by the writer in Medford, Massachusetts, in September. The similarity of *S. ternata* to the present species was noted by Petit, and the Medford material, while largely of the typical form, in some cases passes into *S. ternata*. The latter seems to be merely a form in which the cell division is proportionally more rapid than the longitudinal growth, resulting in short, sometimes very short cells; it therefore is not entitled to a separate name, even as a variety.

Page 119, before Subgenus SIROGONIUM, insert,

S. **inconstans**, nov. sp.; P.B.-A., No. 1768. Filamentis circa 30 μ diam.; cellulis 4-15 diam. longis; chromatophoris 3, plus minusve latis, 1-3 circuitus in cellula efficientibus; pyrenoideis magnis, distantibus; cellulis fertilibus manifeste tumidis; dissepimentis nunc replicatis, nunc planis: sporis 45-55μ, plerumque 50 μ diam., 65-125 μ longis, forma breve ovoideis, fusiformibus, vel cylindricis apicibus rotundatis.

Filaments about 30 μ diam., cells 4-15 diam. long, chromatophores 3, more or less wide, with rather large but distant pyrenoids, making 1-3 turns in the cell; fertile cells distinctly swollen; dissepiments sometimes replicate, sometimes plane;

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spores 45-55, usually 50 μ diam., 65-125 μ long, from short ovoid to fusiform or cylindrical with rounded ends. In a stream, Casey, Ill., April 22, 1911, E. N. Transeau. Type in herb. F. S. C.

The most noticeable characteristic of this species is its lack of fixed characters. The diameter of the cell is fairly uniform, but all other characters vary. Some cells are nearly four times as long as others; the chromatophores are sometimes slender and slightly curved, sometimes stouter and closely spiral. The dissepiments are often strongly replicate, almost as often plane, the two forms alternating or occurring at short intervals in the same filament. The spores vary from slightly prolate spheroids to long-fusiform, and quite irregular forms are common. The fertile cell begins to swell as soon as the process toward another filament is formed, and by the time the spore is fairly formed there is quite a space between it and the cell wall. Its nearest ally seems to be *S. Hassallii*, but in that species the chromatophores are uniformly two, there is little variation in the form of the spore, and none in that of the dissepiment; eight diameters seems to be the maximum length of cell. The figures given by Petit and Wolle show lateral conjugation only, while the conjugation in *S. inconstans* as far as observed is scalariform.

Page 121, before Family 2, insert,

5. PLEURODISCUS Lagerheim, 1895, p. 3.

Filaments unattached, cells thin-walled, with 2 parietal chromatophores in the form of rounded, slightly convex disks of uniform thickness, excentrically placed; one central pyrenoid in each chromatophore; usually colored with phycoporphyrin. Reproduction unknown. Only one species.

P. PURPUREUS (Wolle) Lagerheim, 1895, p. 3; Wille, 1909, p. 11, fig. 1. *Zygnema purpureum* Wolle, 1887, p. 224, Pl. CXLIV, figs. 3-7. Filaments 20-25 μ diam., cells 1-2 diam. long, fertile cells not swollen; spores globose, about 20 μ diam. Fig. 1. N. J., Fla. Fig. 1. *Europe.*

Wolle's figures and description leave the nature of the reproduction in this species quite in doubt, and Lagerheim was not able to add anything. The filaments have a somewhat geniculate form, but this is found in *Mougeotia genuflexa*, for instance, without any relation to fruiting. *P. purpureus* appears to occur

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in great quantities under favorable conditions; Lagerheim was able to abstract the coloring matter, which he found to be distinct from all other coloring matters found in algae and which have been isolated and analyzed; he gave it the name of Phycoporphyrin; it is not unlikely that it is the same substance that colors *Zygogonium ericetorum* and some other Conjugales.

Page 121, second paragraph of description of Mesocarpaceae should read,

There have recently been recognized two genera of Mesocarpaceae, *Gonatonema* with a few species, and the large genus *Mougeotia*. Transeau has made a study of the American representatives of *Gonatonema*, the results of which will soon be published. The distinction between the two genera disappears, and all our species of *Gonatonema* should be included under *Mougeotia*, as well as the former genera *Mesocarpus*, etc.

Omit the key to the genera of Mesocarpaceae.

Page 122, to description of Mougeotia add,

Aplanospores with double membrane formed in the middle of an elongated cell, the portions on each side of the spore being shut off by the formation of cross walls.

KEY TO THE SPECIES OF MOUGEOTIA.

1. Fructification by zygospores; aplanospores unknown. 1a.
1. Zygospores exceptional; usual reproduction by aplanospores. 17.

For No. 1 of key substitute 1a.

For Nos. 4-7 of key, substitute,

4. Filaments 15 μ diam. or less. 7.
4. Filaments 20 μ diam. or more. 5.
5. Spore diam. greater than length of tube, spore extending into the cell on each side. 6.
5. Spore occupying the tube only. 9.
6. Spore about 60 μ diam. 5. *M. minnesotensis.*
6. Spore 45 μ diam. or less. 8.
7. Filaments 12-14 μ diam. 7. *M. delicatula.*
7. Filaments 6-10 μ diam. 3. *M. parvula.*

Page 123, add to key,

17. Aplanospores spherical. 19. *M. calcarea.*
17. Aplanospores elongate or subpolygonal. 18.
18. Aplanospores rounded or partly polygonal, swollen on one side only. 20. *M. ventricosa.*
18. Aplanospores ellipsoid, swollen on both sides. 19.

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19. Filaments 5-6 μ diam. 21. *M. Boodlei.*
19. Filaments 10-13 μ diam. 22. *M. Transeaui.*

Page 127, for description of M. CALCAREA (Cleve) Wittrock, 1872, p. 40, Pl. II. substitute,

Filaments 10-14 μ diam., cells 4-20 diam. long, chromatophore ½-⅔ length of cell, with 2-6 pyrenoids, filaments becoming geniculate and cells elongating before spore formation; zygospore globose or angular globose, 21-50, usually 30 μ diam., occupying the whole or part of one or both cells, membrane brown, smooth; aplanospores globose, 17-21 μ diam., more or less deeply immersed in the filament, or even slightly raised from it. Greenland, Börgesen; Canada, A.B.Klugh; Ill., E. N. Transeau. *Europe.*

It was in this species that the different modes of spore formation, supposed to distinguish different genera, were first observed occurring on the same individual; now the characters of *Mougeotia* and of *Gonatonema* are both found here.

In place of Gonatonema, insert,

20. M. **ventricosa** (Wittr.) nov. comb.; *Gonatonema ventricosum* Wittrock, 1878a, p. 16, figs. 1-13; Wolle, 1887, p. 233, Pl. CXLIX, figs. 1-5; *G. notabile* P. B.-A., No. 1174. Filaments 5-7 μ diam., somewhat bent geniculately, cells 6-16 diam. long; aplanospores obliquely elliptic, one side being more convex than the other; seen from the side, elliptic; 22-29×13-16 μ, 12-15 μ thick, yellowish, smooth. Pa., Cal. *Europe.*

21. M. **Boodlei** (W. and G. S. West) nov. comb. *Gonatonema Boodlei* W. and G. S. West, 1897, p. 46; G. S. West, 1904, p. 122, fig. 45, A-F; P. B.-A., No. 1772. Filaments about 5 μ diam., cells 5-45 diam. long, curved; chromatophore occupying ¾ the length of the cell; zygospore quadrate, transversely elongate, 15-23 μ long; free ends somewhat rounded; aplanospore ellipsoid, 23-25×12-15 μ centrally and symmetrically placed in the filament, or projecting slightly on the convex side. Charleston, Ill., E. N. Transeau. *Europe.*

The cells are much elongated before the formation of zygospores or aplanospores; a vegetative cell may be as short as 5 diam. just after division, or as long as 45 diam, just before formation of a spore. The filaments are curved, not geniculate, so that there is usually only one zygospore formed between two filaments.

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22. M. **Transeaui** n. sp. Filamentis 10-13 μ diam. cellulis 5-15 diam. longis, chromatophora equilonga, pyrenoideis 5-6; zygosporis rotundato-quadratis, a latere visis ovatis, 17-23×28-34 μ, conjugatione cellularum dissociatarum formatis, totum spatium utriusque cellulae occupantibus; aplanosporis 16-20×25-30 μ, a facie visis quadratis vel trapezoideis, medio cellulae rectae vel geniculatae formatis; cellulis ante sporae formationem saepe elongatis. Fig. 7.

Filaments 10-13 μ diam., cells 5-15 diam. long, chromatophore of same length, with 5-6 pyrenoids; zygospores rotundate-quadrate, in side view ovate, 17-25×28-34 μ, formed from detached cells, occupying the width of both cells; aplanospore 16-20 × 25-30 μ, in face view quadrate or trapezoidal, formed at the middle of a straight or geniculate cell; cells often lengthening considerably before spore formation. Embarras River, near Greenup, Ill., and in pond in campus of State Normal School, Charleston, Ill. E. N. Transeau. Type in herb. F. S. C.

The zygospores appear to be rare in this species as compared with the aplanospores; in all cases observed they have been produced between two isolated cells, the vegetative filaments breaking up before their formation. This process is common among the Desmidiaceae, and its occurrence here is of interest. The aplanospore appears quadrate and somewhat rounded when formed in a straight cell; when the cell is bent at the middle the spore appears much the shape of the keystone of an arch.

Page 130, before HAEMATOCOCCUS, insert,

C. GLOEOCYSTIFORMIS Dill, 1895, p. 18, Pl. V, figs. 37 and 38; Wille, 1903, p. 143, Pl. IV, fig. 17; Hayden, 1910, p. 41. Cell ovoid, thick-walled, with small conical projection; cilia two, 1½ times the length of the cell; chromatophore extending nearly to base of cilia; division first vertical, then transverse; Palmella state with several enclosed layers. St. Louis Botanical Garden, Mo. Miss A. Hayden. *Europe.*

Page 131, in place of first paragraph, substitute,

Cambridge, Mass., G. T. Moore.

Page 143, for No. 1 of Key to genera of Protococcaceae, substitute,

1. Cells attached at base or with a prolongation. 1a.
1. Cells without basal attachment or prolongation. 3.
1a. Prolongation stout and blunt. 3a. CENTROSPHAERA.
1a. Prolongation when present filiform. 2.

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Page 148, before RHODOCHYTRIUM insert,

3a. CENTROSPHAERA Borzi, 1883, p. 87.

Cells spherical, ellipsoid or somewhat irregular, usually solitary, wall thick, stratified, with a blunt conical or papilliform projection; chromatophore yellowish green, parietal, with one pyrenoid, of granular or radiate structure. Asexual reproduction by numerous biciliate zoospores, that germinate directly to form a vegetative cell. Only one species has been found in America.

C. FACCIOLAAE Borzi, 1883, p. 87, Pl. VII, figs. 1-13; P.B.-A., No. 1773. Cells 25-40 μ diam., lamination in the thick wall and rounded projection quite distinct; zoosporangia up to 80 μ diam.; zoospores 2-3 μ diam. Fig. 2. .Among other algae, especially Myxophyceae, Eastham, Mass., July, 1910, F. S. C. *Europe.*

Page 156, for Nos. 13 and 14 of key, substitute,

13.	Cells arranged in one plane.	14. CRUCIGENIA.
13.	Cells radiating in all directions.	14.
14.	Cells lunate or sickle-shaped.	19.
14.	Cells not lunate nor sickle-shaped.	14a.
14a.	Cells attached directly at one end, radiating.	14a. ACTINASTRUM.
14a.	Cells united to the center by gelatinous strands or stipes.	15.

Page 158, after PALMELLOCOCCUS, insert,

ANKISTRODESMUS Corda, 1838, p. 196, has precedence over Rhaphidium; the American species must now be known as follows:

A. FALCATUS (Corda) Ralfs.

var. ACICULARIS (A. Br.) G. S. West.

var. **fusiformis** (Corda) nov. comb.

A. CONVOLUTUS Corda.

A. **Braunii** (Näg.) nov. comb.

A. SETIGERUS (Schröder) G. S. West.

A. **fractus** (W. and G. S. West) nov. comb.

The following forms can now be added:

A. FALCATUS var. SPIRALIS (W. B. Turner) G. S. West, 1904, p. 224; *Rhaphidium spirale* W. B. Turner, 1893. Cells grouped in bundles of 4 or 8, twisted round each other in the central region of the cells, but free at their extremities. St. Louis, Mo., Hayden, 1910, p. 43. *Europe.*

Var. MIRABILIS (W. and G. S. West) G. S. West 1904, p. 224, fig. 94. E; *Rhaphidium polymorphum* var. *mirabile* W. and G. S. West, 1897. Cells solitary and considerably longer than in the

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typical form, variously curved and often sigmoid; apices very acute; chromatophore completely interrupted in the middle of the cell, and often fragmented; length sometimes over 100 μ, width 2-3.5 μ. St. Louis, Mo., Hayden, 1910, p. 43. *Europe.*

Var. TUMIDUS (W. and G. S. West) G. S. West, 1904, p. 224, fig. 94. D; *Rhaphidium polymorphum* var. *tumidum* W. and G. S. West, 1897, p. 501. Cells solitary or in small aggregates, curved, inflated at the middle; apices very acute; chromatophore with 2, 1 or no pyrenoids; dimensions 61-73×4.5-6.5 μ. St. Louis, Mo., Hayden, 1910, p. 43. *Europe.*

Page 160, for No. 3 of key, substitute,

3. Ends rounded. 4.
3. Ends acute or subacute. 2. *O. lacustris.*
4. Individual cells about 8 μ long, chromatophore divided. 5. *O. novae semliae.*
4. Individual cells 9-35 μ long, chromatophore single. 5.
5. Individual cells 9-13 μ long. 1. *O. Borgei.*
5. Individual cells 22-35 μ long. 6. *O. Naegelii.*

Before CHODATELLA insert,

5. O. NOVAE SEMLIAE Wille, 1879, p. 26, Pl. XII, fig. 3; P. B.-A., No. 1726. Cells 8 × 5 μ, ellipsoidal, wall rather thick; mother cell with 4 or 8 daughter cells, about 25×15 μ. Floating in a pond, Golden Gate Park, San Francisco, Cal., February, 1910, N. L. Gardner. *Europe.*

6. O. NAEGELII A. Braun, 1855, p. 94; P. B.-A., No. 1776. Cells 22-35×10-18 μ, 2 or 4, rarely 8 in the mother cell wall, or solitary, ovoid-oblong; chromatophore single; no distinct thickening at end of cell wall. Cal., Jamaica; also found in jar at laboratory, New Haven, Conn., W. A. Setchell. *Europe.*

Page 161, before N. NAEGELII, insert,

This species was found among other algae in a small pond at Tarpaulin Cove, Naushon, Elizabeth Islands, Mass., July, 1911. The chromatophore was not as usually described for the genus, but there were numerous small chromatophores in each cell, giving a granular appearance, much as in the original figure by Nägeli.

Page 162, for No. 8 of key, substitute,

8. Quadrate. 9.
8. Polygonal. 8a.
8a. One spine at each angle. 9a. *T. caudatum.*
8a. Two spines at each angle. 10. *T. angulosum.*

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Page 164, before T. ANGULOSUM, insert,

9a. T. CAUDATUM (Corda) Hansgirg, 1889, p. 18; Hayden, 1910, p. 45; *T. trigonum* var. *pentagonum* Hayden, 1910, p. 44; *Polyedrium pentagonum* Reinsch, 1888, p. 503; *P. caudatum* Reinsch, 1888, p. 503, Pl. IV, fig. 9. Pentagonal, with one spine at each angle; diam. 14-23 μ; length of spine, 3 μ. St. Louis, Mo., Hayden. *Europe*.

Page 171, before SELENASTRUM, insert,

14a. ACTINASTRUM Lagerheim, 1882, p. 70.

Cells ovoid, oblong or clavate, generally attached by apices to form small, radiating colonies; chromatophore parietal, with pyrenoid. Asexual reproduction by longitudinal and transverse division, daughter cells remaining attached by one end.

A. HANTZSCHII Lagerheim, 1882, p. 70, Pl. III, figs. 25 and 26; Hayden, 1910, p. 43. Cells 10-24×3-6 μ, straight, oblong, apices attenuate or acuminate; membrane delicate, hyaline. Fig. 3. St. Louis, Mo., Miss Ada Hayden. *Europe*.

In key to the species of SELENASTRUM, substitute,

1. Cells less than 10 μ from tip to tip.	1. *S. minutum*.
1. Cells 16 μ or more from tip to tip.	2.
2. Cells about 3 diam. long.	2. *S. Bibraianum*.
2. Cells about 6 diam. long.	3. *S. gracile*.

Before KIRCHNERIELLA, insert,

3. S. GRACILE Reinsch, 1867, p. 65, Pl. IV, fig. 3, a and b; Hayden, 1910, p. 44. Cells long and slender, distance between the acute apices up to 30 μ; largest diam. not over 5 μ. St. Louis, Mo. *Europe*.

Before K. LUNARIS, insert,

KEY TO THE SPECIES OF KIRCHNERIELLA.

1. Distinctly crescent-shaped, with wide opening and acute or rounded apices.	1. *K. lunaris*.
1. More reniform, opening narrow, apices very blunt.	2. *K. obesa*.

After description of var. DIANAE, insert,

2. K. OBESA (West) Schmidle, 1893, p. 83; Hayden, 1910, p. 44; *Selenastrum obesum* W. West, 1892, p. 734, Pl. X, figs. 50-52. Cells stout crescent-shaped to reniform or nearly circular, middle diam. 6-16 μ, apices 1.5-4 μ apart. St. Louis, Mo. *Europe, So. America*.

Page 172, for No. 2 of key, substitute,

2. Cells with external projection.	2a.
2. Cells without external projection.	4.

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2a. Projection single. 3.
2a. Cell with 3 projections. 4a. *C. cubicum.*

Page 173, before C. RETICULATUM, insert,

4a. C. CUBICUM Nägeli, 1848, p. 97, Pl. V, fig. c, 2; Hayden, 1910, p. 43. Cells 8-48, about 18 μ diam., ending in three short projections; colony 20-60 μ diam., rounded or cubical. St. Louis, Mo., Hayden. *Europe.*

Page 180. In the description of the Order ULOTRICHALES, for "cells uninucleate" substitute,

Cells uni-, rarely multinucleate.

In the key, for No. 2, substitute,

2. Cells often colored red or brown. 2a.
2. Vegetative cells true green. 3.
2a. Aerial algae, filiform or disk-shaped. 9. TRENTEPOHLIACEAE.
2a. Algae of submerged stations or on wet ground; the short upright filaments united into gelatinous masses. 10. WITTROCKIELLACEAE.

In No. 4 of key, for ULOTRICHALES, substitute ULOTRICHACEAE.

Page 192, before MICROSPORA, insert,

The description of the filaments of *S. rivularis* as "of few cells" is incorrect, and was based on the statement in Hazen, 1902, p. 166, "composed of 1-3 cells." This must be a misplacement of a character belonging to the rhizoids; see Hazen's plate XXII, showing a many-celled filament.

For No. 2 of key, substitute,

2. Cells less than 15 μ diam. 2a.
2. Cells 16 μ diam. or more. 3.
2a. Cells 1½-3 diam. long. 4. *M. pachyderma.*
2a. Cells 1 diam. long or less. 4a. *M. Lauterborni.*

Page 193, before M. WITTROCKII, insert,

4a. M. LAUTERBORNI Schmidle, 1895, p. 69, Pl. I, figs. 4-6; P. B.-A, No. 1780. Filaments 8-11 μ diam., cells about one diam. long, after division ½-⅔ diam., wall 2-3 μ thick. Beacon Falls, Conn. W. A. Setchell. *Europe.*

Nearly allied to *M. pachyderma*, but with much shorter cells and less distinctly stratified walls.

Page 195, to description of MICROSPORA QUADRATA add: There has been no record of the akinetes of this species, but they

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were abundant in material collected in Orleans, Mass., Sept. 7, 1909, and distributed as P. B.-A., No. 1624. They are spherical, the diameter slightly greater than that of the vegetative cell.

Page 197, for No. 10 of key, substitute,

10. Frond narrowly linear, strongly compressed. 13. *E. marginata.*
10. Frond filiform, 2-8 cells wide, tubular only in the widest parts. 10a.
10. Frond filiform, tubular, of uniform diameter; of numerous series of squarish cells. 14. *E. prolifera* var. *tubulosa.*
10a. Branches very rare; cells 15 μ wide or more. 3a. *E. chaetomorphoides.*
10a. Branches frequent, cells not over 10 μ wide. 3. *E. torta.*

Page 198, under E. TORTA, omit the locality, Barbados.

Before E. PLUMOSA, insert,

3a. E. CHAETOMORPHOIDES Börgesen, 1911, p. 150, fig. 12; *E. torta* Vickers, 1908, Pl. VI, not of Reinbold. Frond filiform, cylindrical, tortuous, simple or very rarely with proliferations; usually solid, of 3 series of cells, two or even one in proliferations, occasionally tubular and of several series; cells subquadrate, 16-18 μ square. Diameter of 3-seriate filament, about 45 μ; of proliferations about 15 μ. W. I.

Forming *Chaetomorpha*-like masses in lagoons, St. Croix, Börgesen. Distinguished from *E. torta* by the cells nearly twice as large, with thinner walls and more regularly placed; the frond cylindrical, not compressed, branches very exceptional and slightly developed, not normal and well developed.

Page 207, after key to the species of MONOSTROMA, insert,

A. Minute fresh water species, frond of no definite outline. a. *M. amorphum.*
A. Marine; rarely also in fresh water. 1.

Page 208, before M. GROENLANDICUM insert,

a. M. **amorphum** nov.; sp. P. B.-A., No. 1730. Fronde minuta, formae irregularis, tenui, membranacea, 6-8 μ crassa; cellulis verticaliter visis rotundato-angulosis, densis, 8-10 μ diam.; in sectione horizontali ovalibus; colore laete viridi; substantia molli, gelatinosa.

Frond minute, of irregular form, delicately membranaceous, 6-8 μ thick; cells seen from the surface rounded, angular, dense,

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averaging 8-10 μ diam.; in cross section horizontally oval; color light green; substance soft and gelatinous. Fig. 4.

Forming a gelatinous mass on a dripping water pipe, campus, University of California, Berkeley, Cal., N. L. Gardner. Type in herb. F. S. C., No. 1633.

From the peculiar character of the station at which this plant occurred, it is quite possible that other characters might be found if it grew in a more normal habitat; in the meantime it seems impossible to place it under any described species, and a name must be given to it.

Page 226, make changes in key as follows:

6. Monoecious. 1. *Oe. cryptoporum.*
6. Dioecious. 6a.
6a. Oogonia 22-25 μ diam. 2. *Oe. rufescens.*
6a. Oogonia 30-38 μ diam. 2a. *Oe. sociale.*
14. Vegetative cells less than 18 μ diam. 14a.
14. Vegetative cells 20-30 μ diam. 11. *Oe. Vaucherii.*
14a. Ooogonia 32-40 μ diam. 10a. *Oe. globosum.*
14a. Oogonia 42-50 μ diam, 10. *Oe. fragile.*
17. Oogonia manifestly swollen, twice as large as filaments or more. 18.
17. Oogonia less swollen, average diam. less than twice that of the filament. 27.
19. Monoecious. 20.
19. Dioecious. 19a.
19a. Vegetative cells 25-30 μ diam. 7. *Oe. cardiacum* var. *carbonicum.*
19a. Vegetative cells 35-45 μ diam. 19. *Oe. rivulare.*
20. Division of antheridial cell vertical. 17. *Oe. upsaliense.*
20. Division of antheridial cell horizontal. 20a.
20a. Oogonium largest near base, oospore filling the lower part. 21a. *Oe. pseudo-Boscii.*
20a. Oogonium ellipsoid, quite filled by oospore. 18. *Oe. Richterianum.*

Page 227, make changes in key as follows:

34. Division of oogonium median or submedian. 35.
34. Division of oogonium superior. 36.
35. Cells with spiral markings. 32. *Oe. punctato-striatum.*
35. Cell walls plain. 35a.
35a. Oogonium globose or subglobose. 33. *Oe. Howardii.*
35a. Oogonium with a whorl of projections. 35b.
35b. Projections mammiform. 38a. *Oe. mammiferum.*
35b. Projections blunt-conical. 38b. *Oe. Itzigsohnii.*

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43.	Oogonia oblong-ellipsoid, ellipsoid or biconic.	44.
43.	Oogonia pyriform.	72. *Oe. sanctae thomae.*
44.	Veg. cells 3-7 μ diam.	44a.
44.	Veg. cells 10-18 μ diam.	39. *Oe. Ahlstrandii.*
44a.	Oogonia biconic or subglobose.	70a. *Oe. pusillum.*
44a.	Oogonia elongate-ellipsoid.	40. *Oe. gracillimum.*

Page 228. For No. 62 in key, substitute,

62.	Oospore globose.	62a.
62.	Oospore ellipsoid.	63.
62a.	Suffultory cell distinctly swollen.	59a. *Oe. Monile.*
62a.	Suffultory cell not swollen.	60. *Oe. macrandrium.*

Page 229. Under description of *Oe. rufescens*, for monoecious, read dioecious.

At end of page add,

2a. OE. SOCIALE Wittrock ex Hirn, 1900, p. 79, Pl. II, fig. 2; P. B.-A., No. 1785. Dioecious; oogonia single, subglobose, pore median; oospore globose or nearly globose, nearly filling the oogonium, membrane smooth; male plants same size as female; antheridia 1-5-?-celled; spermatozoids binate, division vertical.

veg. cell,	9-16 μ diam.,	3-7 diam. long.
oog.,	30-38 μ "	33-42 μ long.
oos.,	28-35 μ "	28-35 μ "
anth. cell,	12-14 μ "	8-11 μ "

Charleston, Ill., E. N. Transeau. *Europe.*

From *Oe. rufescens* it is distinguished by larger dimensions throughout. The two spermatozoids in an antheridium cell also distinguish it from this species, as well as from *Oe. Magnusii* and *Oe. suecicum*.

Page 231, to description of var. CARBONICUM add,

This variety has been collected at Oberlin, Ohio, by F. O. Grover. The dimensions vary much in this material; the vegetative cells are sometimes as much as 50 μ diam., the oogonia as much as 100 μ. Most of the material is of the normal dimensions.

Page 232, before OE. VAUCHERII, insert,

10a. OE. GLOBOSUM Nordstedt ex Hirn, 1900, p. 94, Pl. V, fig. 30; P. B.-A., No. 1675. Monoecious; oogonia single, globose or subglobose, pore superior; oospore globose, nearly filling the oogonium, membrane smooth; antheridia 1-7-celled,

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subepigynous, subhypogynous or scattered; spermatozoids binate, division horizontal; basal cell elongate; terminal cell setiform.

veg. cell,	10-14 μ diam.,	4-7 diam. long.
oog.,	32-40 μ "	32-46 μ long.
oos.,	30-37 μ "	28-37 μ "
anth. cell,	9-12 μ "	4.5-8 μ "

Eastham, Mass., July 6, 1910. *Australia.*

Resembling *Oe. fragile*, but of somewhat smaller dimensions throughout, and with the antheridia often more numerous in a series.

Page. 236. To the localities for OE. RIVULARE, add, Eastham, Mass., July 3, 1910.

Page 238, before OE. MARGARITIFERUM, insert,

21a. OE. PSEUDO-BOSCII Hirn, 1900, p. 291, Pl. XIII, fig. 67; 1906, p. 48, Pl. II, fig. 6; P. B.-A., No. 1678. Monoecious; oogonia single, suboviform, pore superior; oospore ellipsoid-oviform or ellipsoid, filling the lower, swollen part of the oogonium, membrane smooth; antheridia 1-2-celled, subepigynous; spermatozoids binate, division horizontal.

veg. cell,	8-14 μ diam.,	7½-20 diam. long.
oog.,	41-50 μ "	75-105 μ long.
oos.,	38-45 μ "	48-60 μ "
anth. cell,	11-12 μ "	10-11 μ "

Middlesex Fells, Mass., April 3, 1910. *Northern Europe.*

Resembling *Oe. Boscii*, but with vegetative cells longer and more slender, and with smooth membrane to the oogonium; monoecious instead of dioecious.

Page 242. At the end of the note on OE. PACHYANDRIUM, add,

What appears to be the true *Oe. pachyandrium* has been found at Arlington, Mass., June 1, 1910, by Charles Bullard, and was distributed as P. B.-A., No. 1676.

Page 247, before MACRANDRIA, OPERCULATA, ELLIPSOSPORA, insert,

38a. OE. MAMMIFERUM Wittrock ex Hirn, 1900, p. 175, Pl. XXVIII, fig. 165; P. B.-A., No. 1782. Monoecious; oogonia single, rarely 2-, very rarely 3-seriate, ellipsoid, furnished round the middle with a whorl of mammiform projections, operculate, division submedian, narrow; oogonium seen from above stellate,

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with 7-9 rays, incisions between the rays acute, rather deep; oospore globose or subdepressed globose (more rarely depressed globose) not filling the oogonium, membrane smooth; antheridia (sec. Wittrock) unicellular, subepigynous; basal cell usually elongate.

veg. cell,	5-8 μ diam.,	4-7 diam. long.
oog.,	20-28 μ "	20-30 μ long.
oos.,	12-17 μ "	12-16 μ "
anth. cell,	6 μ "	7 μ "

In submerged Sphagnum, Lost Pond, Brookline, Mass., Aug. 6, 1911. *Europe, Africa.*

Resembling *Oe. platygynum*, but monoecious instead of dioecious-nannandrous; the projections of the oogonium distinctly mammiform instead of rounded. The antheridia appear not to have been observed by any one but Wittrock.

38b. OE. ITZIGSOHNII DeBary ex Hirn, 1900, p. 177, Pl. XXVIII, fig. 167. Monoecious, oogonia single, ellipsoid, furnished round the middle with a whorl of 7-10 obtusely conical projections; oospore globose, not filling the oogonium, membrane smooth; suffultory cell not swollen; antheridia (sec. Wittrock) 1-2-celled; terminal cell obtuse or apiculate.

veg. cell,	8-10 μ diam.,	3-6 diam. long.
oog.,	34-40 μ "	32-40 μ long.
oos.,	20-23 μ "	20-23 μ "
anth. cell,	8-9 μ "	9-15 μ "

Holliston, Mass., Charles Bullard. *Europe, Africa.*

Larger in all dimensions than *Oe. mammiferum*, and distinct also by the blunt-conical, not mammiform projections from the oogonium.

Page 249, after note on OE. FLAVESCENS, add,

At Eastham, Mass., a form has been found, and distributed as P. B.-A., No. 1674, in which the suffultory cell is distinctly larger than the other vegetative cells, but all other characters are as in *Oe. flavescens*.

Page 253, before OE. SEXANGULARE, insert,

NANNANDRIA, ANTHERIDIUM EXTERIUS, PORIFERA, ELLIPSOSPORA.

Page 258, after the note on OE. MULTISPORUM, insert,

Material from Wrightville Pond, Charleston, Ill., collected by

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E. N. Transeau, May 25, 1911, agrees with Wood's description and figures, and completes the same on the following points: pore superior; membrane smooth; suffultory cell sometimes similar to the other cells, sometimes slightly larger; antheridium 1-2-celled. These characters being assured, there is no doubt of its distinctness from *Oe. Monile*.

NANNANDRIA, ANTHERIDIUM EXTERIUS, OPERCULATA, GLOBOSPORA.

59a. OE. MONILE Berkeley and Harvey ex Hirn, 1900, p. 229, Pl. XXXVIII, XXXIX, fig. 235; P. B.-A., No. 1783. Dioecious, nannandrous; oogonia single or 2-8, suboviform or subglobose, operculate, division superior, broad; oospore globose or subglobose, nearly filling the oogonium, membrane triple, thick, hyaline; outer membrane smooth externally, median scrobiculate, inner membrane smooth; suffultory cell swollen; vegetative cells often slightly capitellate; basal cell elongate; terminal cell obtuse; dwarf males slightly curved, near the oogonium; antheridium exterior, 1-?-celled.

veg. cell,	9-15 μ diam.,	5-11 diam. long.
suff. cell,	21-29 μ "	1¾-2 diam. long.
oog.,	30-39 μ "	30-56 μ long.
oos.,	28-38 μ "	28-38 μ "
nan. stipe,	9 μ "	25 μ "
anth. cell,	7 μ "	

Tarpaulin Cove, Naushon, Elizabeth Islands, Mass., July, 1911. *Australia*.

No other species of similar dimensions has the combination of slender filaments, much swollen suffultory cell, and seriate globose oospores with thick walls. Forma *Borgei* Hirn occurs in So. America; the type and the other forms and varieties have hitherto been found only in Australia.

Page 258, before OE. LONGATUM, insert,

NANNANDRIA, ANTHERIDIUM EXTERIUS, OPERCULATA, ELLIPSOSPORA.

Page 261, after description of forma AMERICANUM, insert,

Forma PERFECTUM Hirn, 1900, p. 254, Pl. XLIII., fig. 268. Robust, larger in all parts than the type; androsporangia up to 23-celled.

veg. cell,	22-35 μ diam.,	3-9 diam. long.
suff. cell,	37-56 μ "	1½-3½ diam. long.

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oog.,	64-81 μ diam.	72-111 μ long.
oos.,	61-78 μ "	65-85 μ "
andr. cell,	21-30 μ "	15-30 μ "
nan. stipe,	12-16 μ "	55-69 μ "

Hovey's Pond, Oberlin, O., O. F. Curtis.

Asia, Australia, So. America.

Page 263, before OE. ARESCHOUGII, insert,

Forma **major** nova forma; P. B.-A., No. 1672. Cellulis ad 10 diam. longis; oogoniis ad 8-seriatis, ad 40 μ diam.

Cells up to 10 diam. long; oogonia to 8-seriate, to 40 μ diam.

Eastham, Mass., July, 1910. Type in herb. F.S.C., No. 6212.

Page 265, before OE. GIGANTEUM, insert,

70a. OE. PUSILLUM Kirchner in Hirn, 1900, p. 299, Pl. XXIV., fig. 125. Oogonia single, very rarely 2, sub-biconic-ellipsoid or sub-biconic-globose, seen from above circular, margin even; operculate, division median, wide; oospore ellipsoid or subglobose, generally distinctly constricted at the middle, not quite filling the oogonium, membrane smooth; basal cell subhemispherical, not elongate, terminal cell obtuse or obtusely conical.

veg. cell,	3-6 μ diam.,	3-10 diam. long.
oog.,	14-16 μ "	15-25 μ long.
oos.,	11-13 μ "	13-15 μ "
basal cell,	7-8 μ "	7-8 μ "

Charleston, Ill., E. N. Transeau. *Europe, Africa, So. Amer.*

A very minute species, and imperfectly known; it is suspected of being macrandrous-dioecious by Hirn; but he does not give any reason for the suspicion. Its sterile filaments are indistinguishable from those of *Oe. excisum*, but oogonia of the latter have longitudinal folds. Sterile filaments with the characters of *Oe. pusillum* are common on various algae, but oogonia appear to be rare. Sometimes the cells are arranged in a zigzag fashion, reminding one of a string of diatoms.

Page 268, for No. 14 in key, substitute,

14.	Oogonium about 1½ times as long as broad.	15.
14.	Oogonium 1¾ times as long as broad or more.	14a.
14a.	Vegetative cells 13-16 μ diam.	16a. *B. tenuis.*
14a.	Vegetative cells 18-25 μ diam.	19. *B. minor.*

Page 270, before B. POLYANDRIA, insert,

Forma **suberecta** nova forma; P. B.-A., No. 1681. Forma

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typica minor; oogonia 28-32×34-38 μ, depresse-globosis, saepe erectis.

Dimensions smaller than in the typical form; oogonia 28-32×34×38 μ, depressed globose, often erect.

Arlington, Mass., June 1, 1910, Charles Bullard. Type in herb. F. S. C.

To locality for *B. polyandria*, add, Eastham, Mass., Sept. 5, 1909, P. B.-A., No. 1682.

Page 271, to locality for *B. crassiuscula*, add,

East Brewster, Mass., Sept. 8, 1910.

Page 273, to locality for *B. pygmaea*, add,

Lower Pond, Wakefield, Mass., Aug. 13, 1910; P. B.-A., No. 1683.

Page 274, before B. REPANDA, insert,

16a. B. TENUIS Hirn, 1900, p. 368, Pl. LXIII, fig. 388; P. B.-A., No. 1684. Dioecious, nannandrous, gynandrosporous; oogonia suboblong-ellipsoid, erect or more rarely patent, below terminal setae or androsporangia; androsporangia epigynous or more rarely scattered, 1-?-celled; dwarf males near or on the oogonium; antheridium exterior, 1-3-celled.

veg. cell,	13-16 μ diam.,	1½-2½ diam. long.
oog.,	22-26 μ "	42-48 μ long.
andr. cell,	10-12 μ "	13-19 μ "
nan. stipe,	12-14 μ "	18-24 μ "
anth. cell,	7-9 μ "	6-7 μ "

Eastham, Mass. *Northern Europe.*

Smaller in all parts than *B. rectangularis*, with relatively longer cells and oogonium; *B. repanda* is larger and with longer cells.

Page 276, for No. 7 of key, substitute,

7. Filaments enclosed in a definite gelatinous body. 20. CHLOROTYLIUM.
7. No definite gelatinous thallus. 7a.
7a. Sporangia terminal. 19. GONGROSIRA.
7a. Sporangia intercalary. 19a. LEPTOSIRA.

Page 291, before CHLOROTYLIUM, insert,

19a. LEPTOSIRA Borzi, 1883, p. 17.

Frond a dense tuft of subdichotomously branching, tapering

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filaments, partly creeping, partly more or less erect. Cells thin-walled, swollen, short, with parietal chromatophore and no pyrenoid. Any cell may become a sporangium and develop numerous zoospores or zoogametes, escaping through a small hole in the wall of the cell. Zoospores or gametes similar, ovoid, with with 2 cilia and a red stigma. Gametes uniting to form a spindle-shaped zygote, whose development is unknown; zoospore developing to a *Characium*-like plant, the contents dividing into four motionless spores, escaping by dissolution of the cell wall, and germinating to form the normal plant.

L. MEDICIANA Borzi, 1883, p. 17, Pl. II; P.B.-A., No. 1630. Tufts bright green; branches attenuate, ultimate branches short; cells cylindrical to ovoid, 10-20 μ diam., all changing into sporangia or gametangia, the lower cells first; zoospores and zoogametes about 2.5 μ long, developing 20-60 in a sporangium; resting spore about 10 μ diam. Fig. 5.

In a fresh water pool, Nonamesset, Elizabeth Islands, Mass., August, 1909. *Europe.*

Page 297, after

KEY TO THE SPECIES OF STIGEOCLONIUM.

insert,

A. Erect filaments unbranched except at the extreme base. A. *S. subsimplex.*

A. Filaments more or less densely branched throughout. 1.

Page 298, for No. 12 of key, substitute,

12. Filaments 5-7 μ diam. 11. *S. attenuatum.*

12. Filaments 8-11 μ diam. 14.

12. Filaments 12-18 μ diam. 15.

and insert after No. 13,

14. Floating, sparingly branched. 12. *S. stagnatile.*

14. Forming long, attached tufts, luxuriantly branched. 2. *S. amoenum* forma *biforme.*

15. Main filaments cylindrical, cells 3-10 diam. long. 13. *S. subsecundum.*

15 Main filaments moniliform, cells 1-2 diam. long. 15. *S. autumnale.*

A. S. **subsimplex** nov. sp.; P. B.-A., No. 1791. Strato basali e filamentis prostratis, plus minusve intricatis, constante, cellulis 6-8 μ diam., subaequilongis; rotundatis vel subpolygonis latere superiore, rectis inferiore. Filamentis erectis numerosis, saepe ad cellulam singulam filamenti basalis, circa 5 μ diam. ad basin, sursum sensim latioribus, ad circa 8 μ; raro millemetrum longi-

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tudine superantibus, ad apicem acutam sensim attenuatis, pilis terminalibus carentibus; cellulis prope basin circa 2 diam., parte mediana ½-1 diam. longis, prope apicem diametrum multoties superantibus; filamentis cylindricis, interdum parte mediana ad dissepimenta leviter constrictis; cellulis interdum longitudinaliter divisis, pariete plerumque plus minusve obliqua. Filamentis erectis non raro semel vel bis dichotomis inferne, simplicibus superne.

Basal layer of prostrate filaments, more or less entangled, cells 6-8 μ diam., of about the same length, rounded or somewhat polygonal on the upper side, straight on the lower. Erect filaments numerous, often one from each cell of a basal filament, about 5 μ diam. at base, increasing gradually to about 8 μ, seldom over one mm. long, at the apex gradually tapering to an acute tip, without terminal hair; cells near base about 2 diam. long, in the middle part from ½-1 diam., near the apex many diam. long; filaments cylindrical or occasionally slightly constricted at the dissepiments in the stouter part of the filament; cells sometimes divided longitudinally, the wall usually more or less oblique. Erect filaments often once or twice dichotomously branched in the basal part, otherwise simple. Fig. 6.

Forming a bright green coating on old stems of plants in shallow water, "Sunken Meadow," Eastham, Mass., September, 1909. Type in herb. F. S. C., No. 6135.

The popular name given to the station for this plant describes fairly well its appearance, but not its origin. It is a marshy region, formerly connected with the sea, but the connection has been cut off by the formation of sand dunes, and both submarine and fresh water species of algae occur there.*

Amply distinct from our other species of the genus by the distinct differentiation of the prostrate and the erect filaments, and by the absence of the normal *Stigeoclonium* branching, either opposite or alternate. While the prostrate filaments are often somewhat entangled, they can be separated by a little care, and do not tend to form a parenchymatous 'Sohle.' The prostrate filaments are closely applied to the substratum, the lower side being quite even, while on the upper side each cell is more or less irregularly swollen; and the erect filaments proceed from it pectinately, reminding one of the blue-green alga, *Hapalosiphon*.

* See Rhodora, Vol. XII, p. 9, for more particulars.

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The erect filaments are in form and arrangement of cells curiously like the free filaments (assimilators) of the brown alga *Elachista*. No gametes or zoospores were observed when the plant was collected, but some of the shorter cells seemed to be developing into sporangia or gametangia. Visits to the same station were made in 1910 and 1911, but the plant could not then be found.

Page 299, before S. FLAGELLIFERUM, insert,

Forma **biforme** nova forma; P. B. A., No. 1788. Caespitibus laete luteo-viridibus, ad 15 cm. longis, ramosissimis; ramis primariis saepe oppositis, ramificationibus sequentibus alternatis, ramulis obtusis vel brevi-acutis, rare setiferis; cellulis filamentorum primariorum circa 12 μ diam., 3-5 diam. longis, ramorum 10-12 μ diam., aequilongis vel subbrevioribus; ramulorum 5-8 μ diam., ½-1 diam. longis.

Tufts bright yellow green, up to 15 cm. long, much branched, main branches often opposite, subsequent divisions alternate; ramuli blunt or short-pointed, seldom setiferous; cells in main filaments cylindrical, about 12 μ diam., 3-5 diam. long; in branches 10-12 μ diam., as long as broad or somewhat shorter; in ramuli 5-8 μ diam., ½-1 diam. long. In a brook, Tyngsborough, Mass., May 15, 1910. Type in herb F. S. C., No. 6170.

The habit is that of *S. amoenum*, but on examination with the microscope there is at first sight little similarity; the filaments are composed of quite short cells, and the branching is almost entirely alternate. The main filaments are likely to be overlooked, the branching is so luxuriant, but when found they are quite typical of *S. amoenum*, rather long cylindrical cells, with opposite branches issuing from short, interposed cells, sometimes single, sometimes 2 or 3 of these subspherical branch-bearing cells between two longer cylindrical cells. Except on the main filament opposite branching is very rare; branches apparently opposite prove on more careful examination to issue from successive cells, and when the branches are really opposite in position, it will often be found that what appears to be a single cell from which they issue, has been divided by a wall at an angle of about 45° to the axis into two cells. The long-celled main filament usually ends in a series

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of short cells, like those of the branches, the change being abrupt, no cells of medium length interposed between the long and the short. If the distinctive characters here given prove, on further observation, to be constant, it may be better to consider this as a distinct species; for the present, the more conservative course is taken.

Page 302, before DRAPARNALDIA, insert,

15. S. **autumnale** nov. sp.; P. B.-A., No. 1789. Caespitibus subdensis, ad 10 cm. longis, laete viridibus; filamentis primariis 12-15 μ diam., celluis 1-1½, raro 2 diam. longis, forte inflatis; ramis subdistantibus, conformis sed paullo tenuioribus; ramificatione pluries repetita, ramulis deinceps tenuioribus, ultimis non ultra 5 μ diam.; cellulis 2-3 diam. longis, cylindricis, sensim in setas achroas, tenuissimas attenuatis; ramis et ramulis distantibus, alternatis.

Tufts rather dense, to 10 cm. high, bright green; main filaments 12-15 μ diam., cells 1-1½, rarely 2 diam. long, strongly swollen; branches rather distant, similar but slightly more slender, branching several times repeated, branches of successive orders more slender, in the higher orders not over 5 μ diam., cells 2-3 diam. long, cylindrical, gradually tapering into extremely fine, colorless hairs; branches of all orders distant, alternate. On stones in slowly running water, where a brook from Arlington empties into lower Mystic Pond, Mass., October 1, 1910. Type in herb. F. S. C., No. 6294.

The tufts are quite large for the genus; although the branches of all orders are distant, they are so long that the tufts become quite dense. The main filaments have short, strongly swollen cells, the branches of the first order being similar; in successive orders the cells become relatively longer, more nearly cylindrical and of less diam.; the contrast between the stout, moniliform main stem and the fine, confervoid ultimate branches is great, but the transition is gradual; the branching is uniformly alternate. It is hard to say to what described species this is most nearly related; in descriptions of *S. protensa* (Dillw.) Kütz., the long tapering ramuli are emphasized, but *S. protensa* is described as a dwarf species, while tufts of *S. autumnale* are unusually large for the genus. *Conferva protensa* Dillwyn, 1809, Pl. LXVII, might almost be identified with any species

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of *Stigeoclonium*; *S. autumnale* is amply distinct from all of the species figured by Hazen.

Under the name of AERONEMA POLYMORPHA, nov. gen. et sp., Miss Julia W. Snow describes, 1911, p. 67, Pl. XVIII, figs. 9-19, a minute epiphytic alga, whose characters resemble those of early stages of a *Stigeoclonium*. The filaments are branched, but may under certain conditions break up, or may form more or less parenchymatous masses; there are several to many chromatophores in a cell, without pyrenoids: no starch or oil in cell contents, wall of cellulose; reproduction is by means of an amoeboid zoospore with a single cilium, a single chromatophore and a stigma. In the type and only species the filaments are 3-6 μ diam.; 16 or more zoospores are formed in a cell 5-6 $\times$ 2-3 μ. It was first found by the author in Switzerland, afterwards in this country. The figures show a development of the frond quite like a *Stigeoclonium* at the same stage, but the characters of chromatòphores and of formation of spores are quite different. Further study and verification is needed before its position in the system can be settled. Fig. 11.

In the same paper, p. 363, Pl. XVIII, figs. 1-8, Miss Snow describes another new genus, PIRULUS, with one species, P. GEMMATA. The cells are pyriform, 8-12 $\times$ 6-7 μ, may occur singly or may form short, fragile filaments of 12-15 cells; they have a cup-shaped chromatophore and no pyrenoid, from 1-8 nuclei, and occur epiphytic on liverworts and mosses in Guatemala and in Europe. No reproduction is known other than the formation of new cells by budding from the older cells. It is not easy to surmise as to its relationship to other algae. Fig. 10.

In the key to the species of *Draparnaldia*, for No. 3 substitute,

3. Fascicles spherical, the ramuli very regularly and widely forked. 5. *D. Ravenelii.*

3. Fascicles elongate; ramuli irregularly and narrowly forked. 4.

4. Cells of main branches inflated, chromatophore narrow. 3. *D. glomerata.*

4. Cells of main branches cylindrical, chromatophore broad. 4. *D. platyzonata.*

Page 304, before PLEUROCOCCUS, insert,

5. D. RAVENELII Wolle, 1887, p. 110, Pl. XCV; P. B.-A.,

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No. 1792. Main filaments 150-170 μ diam., sparingly branched, branches 60-100 μ diam.; cells ½-1½ diam. long, cylindrical or slightly constricted at the ends; fascicles opposite or whorled, sessile, spherical, the branches radiating, several times forked, with wide axils, 6-8 μ diam. at base, tapering to the acute apex; cells of ramuli ½-2 diam. long. So. Carolina, Ravenel; Charleston, Ill., E. N. Transeau.

Amply distinct from our other species by the stout main filaments, and the absolutely sessile, spherical fascicles, on nearly every cell of the main filaments, the diameter of the fascicle seldom exceeding the diameter of the cell bearing it. The Illinois plants bear numerous large jointed hairs, with a short basal sheath, curiously like the type of hairs with trichothallic growth, found in the Phaeosporeae. No mention of this character is found in the original description of the species, but in authentic material in herb. Farlow, can be seen the collapsed sheathed bases, appearing like rudimentary gemmae; the part of the hair outside of the sheath has disappeared.

Page 310. *Gloeotaenium Loitlesbergerianum*, before known in America only from Trinidad, has been found at Charleston, Ill., by E. N. Transeau, and at Colpit's Bay, Canada, by A. B. Klugh.

Page 314. The typical form of *Coleochaete divergens* was found at Chebacco Lake, Essex, Mass., September 19, 1909, on submerged stems of *Juncus militaris* Bigelow, and was distributed as P. B.-A., No. 1632. The var. *minor* occured at the same lake, on *Batrachospermum*.

Page 321, before Order SIPHONOCLADIALES, insert,

Family 10. WITTROCKIELLACEAE.

Frond consisting of slightly branched, pluricellular, upright filaments, whose cells can develop unicellular hairs. Cells multinucleate, with green or yellow net-shaped parietal chromatophore, sometimes developing an orange-colored oil. Reproduction by akinetes and by aplanospores, the latter formed in numbers by free division in an aplanosporangium; zoospores and gametes unknown. Only one genus.

WITTROCKIELLA Wille, 1909a, p. 16.

Filaments imbedded in gelatin, forming a cartilaginous expansion; pluricellular rhizoids produced below, uni-, rarely

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bicellular hairs above. Chromatophore with numerous pyrenoids; aplanosporangia formed from terminal cells of filaments. Only one species.

W. PARADOXA Wille, 1909a, p. 16, Pls. I–IV; P. B.-A., No. 1631. Branches short, arising usually from upper ends of cells; cells spherical, ovoid, or elongate, 20-40 μ diam.; upper cells usually orange-yellow. Akinetes formed from upper vegetative cells, about 60 μ diam., germinating immediately or after a resting period; aplanosporangia 30-60 μ diam., formed from swollen upper cells of filaments; aplanospores spherical, 5-10 μ diam. Fig. 8. Among various algae forming a coating on ground frequently submerged by salt or brackish water, Nonamesset, Elizabeth Islands, Mass., August 9, 1909. G. T. Moore. *Europe.*

In this species are united characteristics of the different families Trentepohliaceae, Chaetophoraceae and Cladophoraceae; the position here given it is in the nature of a compromise.

Page 329, before R. KOCHIANUM, insert,

Forma **longiarticulatum** nova forma; P. B.-A., No. 1735. Cellulis 2-6 diam. longis. Cells 2-6 diam. long. San Mateo Beach, Cal., N. L. Gardner. Type in herb. F. S. C., No. 2100.

Page 345, before C. FASCICULARIS, insert,

Forma **stricta** nova forma; P. B.-A., No. 1583. Ramis et ramulis virgatis, minime recurvis.

Branches of various orders virgate and not much recurved; quite different in habit from the typical form, but otherwise the same. Southern California.

Page 346, as a foot note to *C. ovoidea*, add,

C. MACDOUGALII Howe, 1911, p. 491, Pl. XXXIII, fig. 7. This species is compared by its author with *C. Hutchinsiae* (Dillw.) Kütz. and *C. ovoidea* Kütz., but is considered distinct from both. A specimen kindly furnished by the author shows that it is amply distinct from the *C. Hutchinsiae* of England and France, N. J. and Barbados. It is, however, quite close to the California plant given as *C. ovoidea* by the writer, 1909, p. 346, and would have been placed there without question. It may well be that it is distinct from the *C. ovoidea* of Europe, which appears to be a little known species. The California plant is larger in all dimensions, less moniliform, and with long excurrent axes. A comparison of specimens from various stations shows much variation in the two last particulars, but all are much stouter then *C. ovoidea* as originally described. It often varies in the direction of *C. microcladioides* Collins, with denser and more fasciculate branching.

Page 348, before C. PROLIFERA, insert,

Under *C. graminea* should be included the plant from Cali-

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fornia distributed as P. B.-A., No. 1690, as *C. erecta*. The younger branches are usually 2-4 cells long and unbranched, but apparently branches are formed later at each dissepiment, and in the older part of the plant a single long cell extends from one branch to the next. It is probably a case where the ramification, usually simultaneous with the cell division, lags a little behind.

Page 351, under *C. canalicularis*, note,

A plant agreeing with this species, as distributed by European authorities, has been collected at St. Louis, Mo., by G. T. Moore, and has been distributed as P. B.-A. No. 1689.

Page 360, before S. SAXATILIS, insert,

Forma **limitanea** nova forma; P. B.-A., No. 1736. Caespitulis 1-3 cm. altis; filamentis circa 75 μ diam. prope basin, apice ad 150 μ; cellulis ut plurimum 4-8 diam. longis, pariete crassa.

Tufts 1-3 cm. high; filaments about 75 μ diam. near base, to 150 μ at apex; cells mostly 4-8 diam. long, wall thick. On a stone wall, just above high water mark, with fresh water running over it. Fort Point, San Francisco, Cal., February, 1910, N. L. Gardner. Type in herb. F. S. C., No. 2160.

The typical form of this species grows on exposed rocks in the lower litoral, and reaches a length of over a decimeter; in forma *limitanea* the filaments are very short, but stouter than the average in the typical form.

Page 363, for Nos. 2 and 3 of key, substitute,

2. Main filament seldom under 150 μ diam. 1. *P. aequalis* var. *floridensis*.
2. Main filament seldom reaching 140 μ diam. 2a.
2a. Vegetative cells cask-shaped. 3.
2a. Vegetative cells and akinetes cylindrical. 1a. *P. Mooreana*.
3. Special helicoidal cells frequent. 3. *P. Cleveana*.
3. Special helicoidal cells wanting or very rare. 3a.
3a. Branches of one order, seldom more; intercalary akinetes about 80 μ diam. 2a. *P. kewensis*.
3a. Branches of three orders; intercalary akinetes about 115 μ diam. 2. *P. oedogonia*.

Before P. OEDOGONIA, insert,

1a. P. **Mooreana** nov. sp.; Hayden, 1910, p. 47; P. B.-A., No. 1637. Filamentis primariis 95-140 μ diam., ramis solitariis vel oppositis, 75-100 μ diam., elongatis, sensim attenuatis,

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plerumque in akinetam desinentibus; cellulis plerumque longis, ad 20 diam., interdum multo brevioribus, precipue inter duas akinetas; akinetis intercalaribus diametrum filamentorum aequantibus vel paullo minus, stricte cylindricis, 1½-4 diam. longis; akinetis terminalibus ad plurimos ramulos, conicis, circa 50 μ diam., ad basin subrotundatis, 125 μ longis, ad apicem rotundatis; akinetis et cellulis vegetativis plerumque regulariter alternantibus, ramulis longioribus brevioribusve saepe ex akinetis exeuntibus, interdum cum akinetis continuis; vel ex akineta ramulo, akinetis et cellulis vegetativis alternatim positis, constante; akinetis ramuliferis ceteris plerumque brevioribus.

Main filaments 95-140 μ diam., branched, branches solitary or opposite, 75-100 μ diam., long, gradually tapering, usually ending in an akinete; cells usually long, up to 20 diam., but sometimes much shorter, especially when between two akinetes; intercalary akinetes of about the same diam. as the filaments or slightly smaller, strictly cylindrical, 1½-4 diam. long; terminal akinetes on most of the branches, conical, about 50 μ diam. at the somewhat rounded base, 125 μ long to the rounded tip. Akinetes and vegetative cells usually in regular alternation, longer or shorter branches frequently proceeding from akinetes, often continuous with the akinetes; or the branch from the akinete may consist of alternated akinetes and vegetative cells; branch-bearing akinetes usually shorter than the others. Fig. 9. In a pond in which Japanese plants were cultivated, Missouri Botanical Garden, St. Louis, Mo., G. T. Moore. Type in herb. F. S. C.

The nearest relative seems to be *P. sumatrana* (Mart.) Wittr., from which it differs by the abundant terminal akinetes, and especially by the branches proceeding from the akinetes.

Page 364, before P. CLEVEANA, insert,

P. KEWENSIS Wittrock, 1877, p. 52, Pl. I, fig. 8; II, figs. 1-12; III, figs. 1-9; IV, figs. 2-11; V, figs. 9 and 10; P.B.-A., No. 1635. Main filaments about 60 μ diam., branches of one, rarely of two orders; akinetes single, intercalary or terminal, intercalary elongate-cask-shaped, about 80×200 μ; terminal cask-shaped with blunt-conical apex, about 85×220 μ. In a small pond in a pasture, Oberlin, Ohio, Oct., 1909, Miss S. P. Nichols.

A well known species of greenhouses, etc., in Europe, but of which the native station is unknown. From the character of the plants in connection with which it occurs, it has been sup-

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posed to be tropical or subtropical, and its occurrence in Ohio, apparently native, is rather surprising.

Page 371, after Key to the genera of Valoniaceae, insert,

A. Endophytic or epiphytic. A. BLASTOPHYSA.
A. Not endophytic nor epiphytic. 1.

After the key, insert,

BLASTOPHYSA Reinke, 1889a, p. 27.

Frond a swollen, multinucleate cell or a series of such cells, of irregular shape, bearing on the upper side long colorless bristles; chromatophores numerous disks, sometimes with a pyrenoid. Reproduction by ovoid zoospores with 4 cilia and 1 or 2 stigmata, formed in large numbers in a cell, escaping by a neck-like opening.

A genus of epi- or endophytic algae of somewhat doubtful relationship, perhaps as much allied to the Chaetophoraceae as to the Valoniaceae; three species are known, all marine.

B. RHIZOPUS Reinke, 1889a, p. 27, Pl. XXIII; Börgesen, 1911, p. 151. Cells 50-120 μ diam., each producing several erect bristles; also horizontally directed long, slender, colorless tubes, from which new normal cells may arise. Fig. 12. On or in various algae; found at St. Croix in *Nemalion Schrammi*. *Europe*.

Page 388 for C. ELONGATUM, substitute,

C. DECORTICATUM (Woodw.) Howe, 1911, p. 494; *Ulva decorticata* Woodward, 1797, p. 55; and add to localities, La Paz, Baja California. M. A. Howe.

Page 389, for C. MUCRONATUM, substitute,

C. FRAGILE (Suringar) Hariot, 1888, p. 32; *Acanthocodium fragile* Suringar, 1870, p. 23, Pl. VIII.

For Var. CALIFORNICUM J. G. Agardh, substitute,
Var. CALIFORNICUM (J. Ag.) Hariot, 1891, p. 215.

For Var. NOVAE ZELANDIAE J. G. Agardh, substitute,
Var. **novae zelandiae** (J. Ag.) nov. comb.

Before AVRAINVILLEA, insert,
Subfamily UDOTOIDEAE.

Page 390, for No. 2 of key, substitute,

2. Surface of flabellum smooth or smoothish. 2a.
2. Surface of flabellum velutinous, spongy or strigose. 3.

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2a. Filaments 20-30 μ diam., not much tapering. 3a. *A. Elliottii.*
2a. Filaments 6-35 μ diam., much tapering upwards. 3. *A. levis.*

Page 391, before A. LONGICAULIS, insert,

A. ELLIOTTII Gepp, 1911, p. 35, Pl. XII, figs. 99 and 100; *A. sordida* Murray and Boodle, 1889, p. 70, in part. Rhizome erect, about 5 cm. high, passing into stipe 1-4 cm. long, slightly compressed, simple, expanding suddenly into the broad flabellum 4-5 cm. long, 5-10 cm. wide, lobed, sometimes split nearly to the base, zonate, minutely wrinkled; filaments cylindrical, sometimes slightly torulose, 20-30 μ diam., of nearly uniform diameter throughout. Granada.

This species is based on a single collection at the island of Granada in 1887, the specimens now preserved in the British Museum; *A. sordida* Murray and Boodle was founded on this and two other specimens, now pretty clearly all three distinct species. The Gepps retain the name *A. sordida* for one of these, which is identical with *A. levis* Howe; but as they express the opinion that the name *A. longicaulis* will ultimately have to be substituted for *A. sordida*, and as the question between the latter name and *A. levis* is rather a complicated one, it will do no harm to retain Howe's name for the present. As to our other species of *Avrainvillea*, the Gepps use *A. Mazei* Murray and Boodle in place of *A. longicaulis*, and accept *A. asarifolia* Börgesen; the other names are not changed. Börgesen, 1911, p. 148, reports having examined the original specimen from Guadeloupe, determined as *Chlorodesmis comosa* by Mazé and Schramm, and to have found it to be *Vaucheria dichotoma*; he also considers the plant formerly doubtfully named *Avrainvillea comosa* by him, to be also *V. dichotoma*.

Page 392, in place of the key to the species of *Penicillus*, insert,

1. Surface of stipe spongiose or velutinous-tomentulose under a hand lens; ultimate branchlets of corticating filaments elongate, taper-pointed. 2.
1. Surface of stipe compact, indurated, smooth or minutely granulose under a hand lens; ultimate branchlets of corticating filaments short-oblong, obtuse, truncate or capitate. 3.
2. Filaments of head 150-320 μ diam. 4. *P. pyriformis.*
2. Filaments of head 500-900 μ diam. 2. *P. dumetosus.*
3. Filaments of head 135-250 μ diam. 1. *P. capitatus.*
3. Filaments of head 300-500 μ diam. 3. *P. Lamourouxii.*

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This key and that of the next following genus, *Rhipocephalus*, were prepared for use in the North American Flora by Dr. M. A. Howe, to whose kindness I am indebted for permission to make use of them here. Dr. Howe's study of the living plants has done much to clear up the confusion formerly existing as to the species of these genera. Gepp, 1911, gives full descriptions of all our species, with figures. The name *P. dumetosus* is of Blainville, 1834, not of Decaisne, 1842. *P. capitatus* is divided into the typical form, *Corallina Penicillus* Ellis and Solander, 1786, with filaments 100-200 μ diam., and stipe 4-8 cm. long; and forma *elongatus*, *P. elongatus* Decaisne, 1842, p. 97, with narrow head, filaments 200-300 μ diam., stipe 6-15 cm. long.

Page 393, before R. PHOENIX, insert,

KEY TO THE SPECIES OF RHIPOCEPHALUS.

1. Filaments of head 55-90 μ diam. towards apices, rather firmly and persistently coherent, in always easily recognizable flabella. 1. *R. Phoenix*.

1. Filaments of head 100-230 μ diam. toward apices, lightly and transiently coherent, the flabella scarcely recognizable at maturity. 2. *R. oblongus*.

Page 394, before UDOTEA, insert,

2. R. OBLONGUS (Decaisne) Kützing, 1849, p. 506. *Penicillus oblongus* Decaisne, 1842, p. 97. Stipe to 7 cm. high, about 6 mm. wide, somewhat compressed, penetrating ¾ of head, much calcified, usually smooth; head to 5 cm. long, 1-3 cm. broad, with a cup-shaped depression at top in which arise the young flabella; flabella cuneate, to 15 mm. long, slightly calcified, composed of non-adherent, dichotomously branched filaments, 160-200 μ diam. above, 200-350 μ at base. Bahamas.

Easily distinguished by the flabella which, while plane and monostromatic in both species, are composed of filaments firmly laterally coherent in *R. Phoenix*, nearly or quite free in *R. oblongus*, the ultimate divisions in the latter 100-230 μ, 55-90 μ in the former. It is not, however, always easy to distinguish from *Penicillus capitatus*. In old plants of *R. oblongus* the filaments of the different flabella are much entangled, and only in the youngest flabella, at the growing point in the apical cup, can the true arrangement be distinguished. When the frond is dried, especially if pressed, the apical depression is often indistinguishable, and there is much resemblance to *Penicillus*.

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Page 394, for No. 4 of key, substitute,

4.	Flabellum with a cortex of spinulose branches.	4a.
4.	Flabellum uncorticated.	5.
4a.	Spinulose branches in close whorls.	4a. *U. verticillosa.*
4a.	Spinulose branches subsecund or irregular.	4. *U. spinulosa.*

Page 395, before U. FLABELLUM, insert,

4a. U. VERTICILLOSA Gepp, 1909, p. 269; 1911, p. 128, Pl. II, figs. 16, 19, Pl. III, figs. 23, 25. Frond to 10 cm. high, calcified; stipe 1.5-4 cm. long, 1 mm. thick, apex sometimes flattened; flabellum with a cordate, rarely cuneate base, to 10 cm. wide, sometimes striate and zonate; surface very minutely cristate-spiculose or granulose; filaments 30-60 μ diam., parallel, not contiguous, monostromatic at apex, pluriseriate below, sparingly dichotomous, not constricted, lateral appendages in close verticils, especially in upper parts of filaments, many pronged and acute. W. I.

Page 396, for U. ARGENTEA, substitute,

6. U. OCCIDENTALIS Gepp, 1911, p. 127, Pl. II, fig. 18; Pl. VII, figs. 63-65. Frond up to 8 cm. high; stipe simple, terete, to 1 cm. high, about 1.5 mm. thick; frond ovate from a cuneate base, more or less proliferous, zoned, faintly striate. Frond filaments 30-45 μ diam., bearing capitate branchlets 70-120 μ long, lateral appendages two or three times dichotomous, ending in short, densely set lobes. Danish W. I.

Nearly allied to *U. argentea*, but considered distinct by the smaller frond filaments (in *U. argentea* they are 40-60 μ diam.), the shorter branchlets (in *U. argentea* they are 100-180 μ long).

Page 399, before H. LACRIMOSA, insert,

Var. OPUNTIOIDES Börgesen, 1911, p. 144, fig. 11. Segments large, broadly suboval-reniform, often distinctly crenulate at the upper margin, or even trilobed. St. Croix.

The form of the segments is much like that in *H. Opuntia*, but they are in one plane, and the structure is that of *H. gracilis*.

Page 400, before H. DISCOIDEA, insert,

Var. PLATYDISCA (Decne.) Barton, 1901, p. 14, Pl. I, fig. 2; Börgesen, 1911, p. 134; *H. platydisca* Decaisne, 1842, p. 90. Upper segments large, thin, reniform, discoid or transversely oblong. St. Thomas, W. I., in open sea at 20-30 meters. Börgesen.

To localities for *H. discoidea* add La Paz, Baja California, Howe.

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Before H. OPUNTIA, insert,

Var. PLATYLOBA Börgesen, 1911, p. 135, fig. 3. Segments broader, up to 4 cm., lightly calcified, especially when young. St. Thomas, W. I., in open sea at 20-30 meters. Börgesen.

H. Tuna var. *platydisca* and *H. discoidea* var. *platyloba*, appear to be deep sea forms of their respective species.

Page 411, for Nos. 1 and 2 of key, substitute,

1. Stolon and fronds filiform, not distinctly differentiated. 2.
1. Stolon and fronds different in character. 3.
2. Divisions of fronds filiform, ramuli not differentiated. 1. *C. fastigiata.*
2. Fronds with distinct, distichous ramuli. 16. *C. Vickersii.*

Page 421, for 16. C. AMBIGUA, substitute,

16. C. VICKERSII Börgesen, 1911, p. 129, fig. 2; *C. ambigua* Vickers, 1908, p. 25, Pl. XXXVII; not *C. ambigua* Okamura, Algae Japonicae Exsicc., No. 95. Stolon more or less distinct, irregularly curved, creeping; frond ascending, terete, with subcylindrical, distichous, rarely irregularly placed opposite or alternate ramuli, the longer often with forked apices. Barbados; St. Croix. *Japan.*

The question of the difference between this species and *C. ambigua* is treated at length by Börgesen, l.c. He considers that Okamura (1879) confused two species, figs. 3-6 in the plate being *C. ambigua* as described by him, but figs. 7-10 the same as Miss Vickers' plate and description, and the new name is given to the latter form. Its place in the genus is near *C. fastigiata.*

Page 461, fig. 128, for Boodlea compacta, read Boodlea composita.

Fig. 148, for after Börgesen, read after Howe.

Additional species distributed in the Phycotheca Boreali-Americana:

Botrydium Wallrothii.	1834.
Bulbochaete intermedia forma supramediana.	1680.
" polyandria.	1682.
" pygmaea.	1683.
" setigera.	1732.
Cladophora canalicularis	1689.
" crystallina.	1581.
" delicatula.	1582.

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Cladophoropsis membranaceus. 1634.
Coelastrum cambricum. 1669.
Coleochaete orbicularis. 1733.
Dichotomosiphon pusillus. 1587.
Draparnaldia platyzonata. 1686.
Endoderma viride. 1626.
Endophyton ramosum. 1627.
Gloeocystis scopulorum. 1579.
Ineffigiata neglecta. 1621.
Monostroma orbiculatum var. varium. 1575.
Mougeotia quadrangulata. 1572.
Neomeris annulata. 1584.
" Cokeri. 1585.
" mucosa. 1586.
Neophrocytium Agardhianum. 1777.
Oedogonium Boscii var. occidentale. 1671.
" cardiacum var. carbonicum. 1781.
" echinospermum. 1673.
" multisporum. 1784.
" platygynum. 1677.
" sexangulare. 1679.
" upsaliense. 1576.
" Vaucherii. 1786.
Oocystis crassa. 1775.
" solitaria forma major. 1727.
Ophiocytium capitatum. 1766.
Pediastrum duplex. 1574.
" tetras. 1623.
Pilinia endophytica. 1838.
" Reinschii. 1685.
Pithophora oedogonia. 1636.
Pseudodictyon geniculatum. 1628.
Rhaphidium falcatum var. aciculare. 1774.
Rhizoclonium riparium var. validum. 1688.
Siphonocladus tropicus. 1638.
Sorastrum spinulosum. 1778.
Spirogyra insignis. 1570.
" Juergensii. 1769.
" setiformis. 1724.
Stichococcus rivularis. 1833.
Stigeoclonium lubricum var. varians. 1790.
" tenue. 1731.
Trentepohlia abietina. 1687.
Ulvella prostrata. 1629.
Urococcus insignis. 1578.
Zoochlorella conductrix. 1622.

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LIST OF WORKS TO WHICH REFERENCE IS MADE.*

Börgesen, F. 1911. Some Chlorophyceae from the Danish West Indies. Bot. Tidsskrift, Vol. XXXI, p. 127.

Collins, F. S. 1909. The Green Algae of North America. Tufts College Studies, Vol. II, p. 79.

Corda, A. J. C. 1838. Almanach de. Carlsbad de 1838, p. 196. Prague.

Dill, E. A. 1895. Die Gattung Chlamydomonas und ihre nächsten Verwandten. Prings. Jahrhb., Vol. XXVIII.

Ellis, J., and Solander, D. 1786. The Natural History of many curious and uncommon zoophytes. London.

Gepp, A. and E. S. 1909a. Journal of Botany, Vol. XLVII, p. 269.

1911. The Codiaceae of the Siboga Expedition. Siboga-Expeditie, Monogr. LXII. Leiden.

Hariot, P. 1888. Mission scientifique du Cap Horn, 1882-83. Vol. V, Botanique. Algues. Paris.

1891. Liste des algues marines rapportées de Yokoska (Japon) par M. le Dr. Savatier. Mem. Soc. Sci. Nat. Cherbourg, Vol. XXVII, p. 211.

Hayden, Ada. 1910. The algal flora of the Missouri Botanical Garden. 21st annual report of the Miss. Bot. Garden, p. 25.

Howe, M. A. 1911. Phycological Studies. V. Some marine algae of Lower California, Mexico. Bull. Torrey Bot. Club, Vol. XXXVIII, p. 489.

Lagerheim, G. von. 1895. Ueber das Phycoporphyrin. Christiana Vid. Selsk. Förh., No. 5.

Snow, Julia W. 1911. Two epiphytic algae. Bot. Gazette, Vol. LI, p. 360.

Schmidle, W. 1895. Weitere Beiträge zur Algenflora der Rheinebene und des Schwarzwaldes. Hedwigia, Vol. XXXIV, p. 66.

* Works included in the similar list in Collins, 1909, are not given in the present list; but references to them in the text use the abbreviations of the 1909 list.

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Suringar, W. F. R. 1870. Algae Japonicae Musei Botanici Lugduno-Batavi. Haarlem.

Turner, W. B. 1893. Algae aquae dulcis Indiae orientalis. Kgl. Vet.-Akad. Handl., Vol. XXV, No. 5.

West, W. 1892. Algae of the English Lake District. Jour. Roy. Micr. Soc., p. 734.

Wille, J. N. F. 1909. Conjugateae und Chlorophyceae. Nächtrage zu Engler und Prantl, Natürliche Pflanzenfamilien. Teil 1, Abt. 2.

1909a. Ueber Wittrockiella, nov. gen. Nyt Mag. f. Naturv., Vol. XLVII, p. 1.

Woodward, T. J. 1797. Observations upon the generic character of Ulva, with descriptions of new species. Trans. Linn. Soc., Vol. III, p. 46.

EXPLANATION OF PLATES.

PLATE I

1. Pleurodiscus purpureus, after Lagerheim. 500×1.
2. Centrosphaera Facciolaae, after Borzi. 450×1.
4. Monostroma amorphum, by Lambert. 500×1.
5. Leptosira Mediciana, after Borzi. 630×1.
6. Stigeoclonium subsimplex, by Lambert. 700×1.
7. Mougeotia Transeaui, after Transeau. 400×1.
9. Pithophora Mooreana, by Lambert. 30×1.

PLATE II

3. Actinastrum Hantzschii, after Lagerheim. 600×1.
8. Wittrockiella paradoxa, after Wille. Aplanosporangium, 300×1; other figures, 150×1.
10. Pirulus gemmata, after Snow. 800×1.
11. Aeronema polymorpha, after Snow. 800×1.
12. Blastophysa rhizopus, after Reinke. 800×1.

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DIDYMOSPORANGIUM REPENS.

New Genus and Species of Chaetophoraceae.

By F. D. Lambert.

Occurrence. In May, 1911, when I was at the Naples Zoological Station* working on the structure and development of the 'Blazenzellen' in Antithamnion and Bonnemaisonia, one of the station collectors brought to me one day a small amount of Antithamnion plumula, on a few specimens of which I discovered the few minute plants upon which this description is based. While it was known that this material had been collected at no great distance from the Station, it was not only impossible to discover the exact locality where the specimens had been found, but also equally impossible to find any further trace of the plant on any of the Antithamnion material which was brought to me in considerable quantity after that date. Moreover, a careful examination of living algae of a number of other genera failed to disclose other specimens of it. The few specimens of Antithamnion on which the plants were growing were kept alive for a few days in aquaria, during which time they were under almost continuous observation. Finally the Antithamnion specimens on which the material was growing were killed and mounted in toto in glycerine-gelatine on slides to be preserved as type specimens in my herbarium. All drawings and measurements were made from living specimens with the oil-immersion lens and camera lucida.

Morphology. The plant in the vegetative condition consists of a short and usually straight, naked, branching filament of a few cylindrical cells of uniform diameter which grow closely applied to the cell walls of the Antithamnion (see figs. 1, 3, 4, 6, 7, 9). When the filament occurs at the end of a branch it often curves completely around the tip of the terminating cell (figs. 2 and 12). Each cell contains a single chromatophore, light green in

* I hereby acknowledge my indebtedness to the officers of the Carnegie Institution for the privilege of occupying the Carnegie Table at the Station, aud to the staff of the Station for the many facilities and courtesies extended to me.

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color, which completely covers the cell wall, to which it is closely applied, and a comparatively large and conspicuous pyrenoid (fig. 1 p). The cell nucleus is occasionally sufficiently visible to be located without staining (fig. 1, n). The filaments branch very simply, the branches very often consisting of not more than a single cell (figs. 3 and 6). Branches of the second order were not observed. The branches arise as outgrowths from the ends of the cells, usually in the immediate neighborhood of a septum (fig. 3). Branching was not seen in filaments less than four cells long. Growth is terminal, the filaments elongating at both ends. Cell division is always preceded by division of the pyrenoid in the usual manner of elongation and constriction. The plane in which the pyrenoid divides, however, is not always at right angles to the longitudinal axis of the cell. Cells are often seen in which the daughter pyrenoids must revolve about each other through an angle of from 45° to 90° before they come to lie in the position which they must occupy preceding the development of the wall which is to separate the two daughter cells (figs. 11 and 14).

REPRODUCTION. The plants reproduce by means of bi-ciliate, motile cells, formed in sporangia which, apparently, may be developed from any or all the cells, development taking place in such manner that the sporangia occur in pairs (see figs. 1,2,6,9,12). Although, owing to scarcity of material, the entire development of the sporangium could not be followed in all its stages, the process of development seems to be as follows: Sporangium development begins in or near the middle of the filament. One or more cells cease to grow in length, and each divides by two successive divisions in such way that each of the original cells gives rise to four cells. These cells then increase in transverse diameter, elongating in a direction at right angles not only to the longitudinal axis of the filament itself, but also at right angles to the plane of the wall of the Antithamnion cell or cells on which they are growing. Moreover, these cells which thus arise in groups of four from the original cells of the filament, stand in pairs which are very evident in some specimens and easily recognizable in all. This development, beginning in the middle of a

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filament, may and often does extend toward either or both ends, the entire filament thus becoming transformed into sporangia (figs. 2 and 9). Figure 1 represents a typical specimen in which the sporangia have been developed from the middle cells of the filament and show the characteristic paired arrangement. That there may be a deviation from the manner of development above described is evident from specimens in which the sporangia occur in odd numbers (fig. 8), a condition, however, which I regard due to possible irregularities in the preliminary division or divisions of the original cells of the filament which give rise to the sporangia. Occasionally one of the sporangia becomes crowded out of line and extends in a plane different from that of all the others (fig. 1). In such instance, however, it is not difficult to distinguish between such an aberrant sporangium and a real branch, the latter always being much longer. After the paired sporangia have become fully elongated, the protoplast of each divides equally in a plane transverse to the longer axis of the sporangium and parallel to the axis of the main filament (figs. 2 and 15). The pyrenoids of the paired sporangia usually lie on the sides of the sporangia which are opposite their contiguous faces. This position of the pyrenoids in sporangia of such a developmental stage renders the paired condition of the sporangia particularly conspicuous (see figs. 1, 2 6, 12.) By a second division in a plane parallel to the first, the two protoplasts of each sporangium become divided into approximately equal parts which very soon become organized into motile cells of the usual pyriform type, each with a single large cup-shaped chromatophore containing in its thickened base a single, large and conspicuous pyrenoid, and near the other end a single, small but distinct stigma (fig. 10). Each of the cells is furnished at the anterior, more pointed end with a pair of flagellae of equal length and about as long as the body of the spore (fig. 16). Occasionally, as result of suppression of one of the divisions of the sporangium protoplast, the mature sporangium contains but three spores, one large one and two smaller but of equal size (fig. 10). This condition is of such rare occurrence that I regard it wholly abnormal. The spores escape from the sporangium through a round hole in its apex (see figs. 13 and 9). Whether the motile cells ever fuse in pairs could not

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be determined, owing to lack of material with which to follow the complete developmental history. Hence nothing can be said concerning the exact nature of the spores, *i. e.*, whether or not they are gametes. The very early stages of germination were not found, the two-celled plants illustrated in figures 4, 5, and 11 being the youngest found.

SYSTEMATIC POSITION. Although it is evident that this plant belongs to the Chaetophoraceae, the absence of hairs of any sort in any known stage in its development classes it with a number of other hairless endophytic and epiphytic forms of the same group, from which, however, it differs sufficiently to warrant placing it in a new genus.

DIAGNOSIS. **Didymosporangium repens** n. g. and sp.

Epiphytica; filamento recto vel curvato, cellulis 1.7-4.5 μ diam., 1-8 diam. longis; cellula terminali vix vel non attenuata, apice rotundata vel subacuta; ramis paucis brevibus, saepe cellulae singulae; cellulis partis centralis filamenti, minus frequenter cellulis omnibus filamenti in sporangia mutatus; sporis quatuor in sporangio. Sporangio 6-10 μ longo, 3.5-9 μ diam.

Epiphytic; filament straight or curved, cells 1.7-4.5 μ diam. 1-8 diam. long; terminal cell little or not at all tapering, apex rounded or blunt point; branches few, short, often of a single cell; cells of the middle of the filament, less commonly all the cells of the filament developing into sporangia; spores four in a sporangium. Sporangium 6-10 μ long; 3.5-9 μ diam.

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EXPLANATION OF PLATE

All figures × 1000

Fig. 1. Typical plant, without branching; middle of filament composed of paired sporangia, one sporangium near centre, slightly out of alignment; *p*, pyrenoid; *n*, nucleus.

Fig. 2. Short filament growing about the tip of an Antithamnion cell; sporangia developing in pairs; *p*, the two daughter pyrenoids of the first division of the sporangium protoplast.

Fig. 3. Typical immature plant, three branches.

Fig. 4. Young plant, two long cells.

Fig. 5. Young plant, two short cells.

Fig. 6. Plant with one branch, sporangia in pairs.

Fig. 7. Immature plant, four cells.

Fig. 8. Plant with uneven number of median sporangia.

Fig. 9. Plant with the sporangia at the two ends further advanced in development than those in the middle of the filament; *s*, empty sporangium with opening at apex.

Fig. 10. Two mature sporangia containing motile cells.

Fig. 11. Plant of two cells; *p*, pyrenoids dividing in planes oblique to the longitudinal axis of the cells.

Fig. 12. Plant with two terminal vegetative cells growing about the tip of an Antithamnion cell.

Fig. 13. Sporangia; *s*, empty, with opening at apex.

Fig. 14. A pair of sporangia; *p*, the two pyrenoids of the first division of the sporangium protoplast, a condition similar to that illustrated in figure 11.

Fig. 15. A pair of sporangia, first division of the protoplast completed.

Fig. 16. Two of the motile cells.

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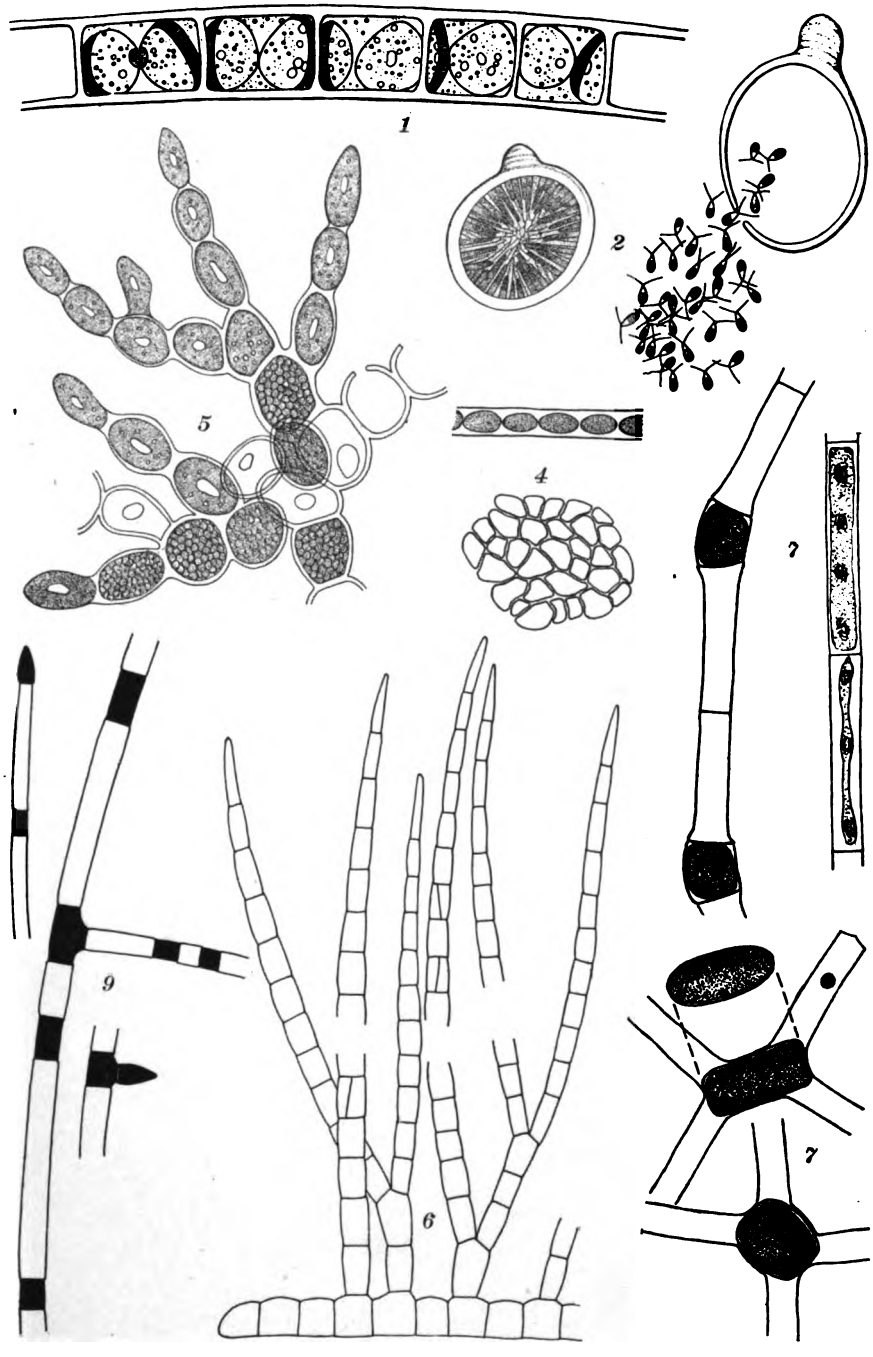

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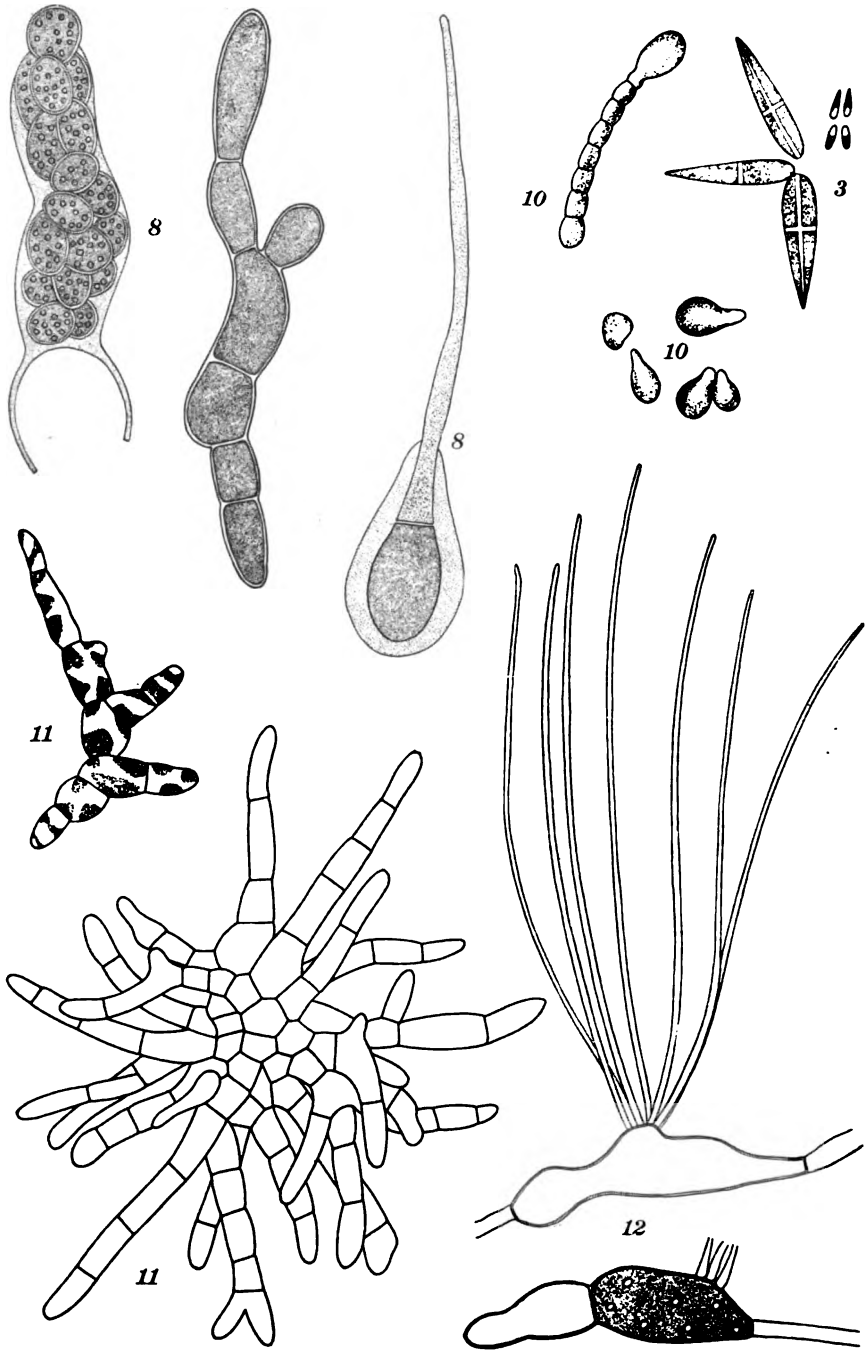

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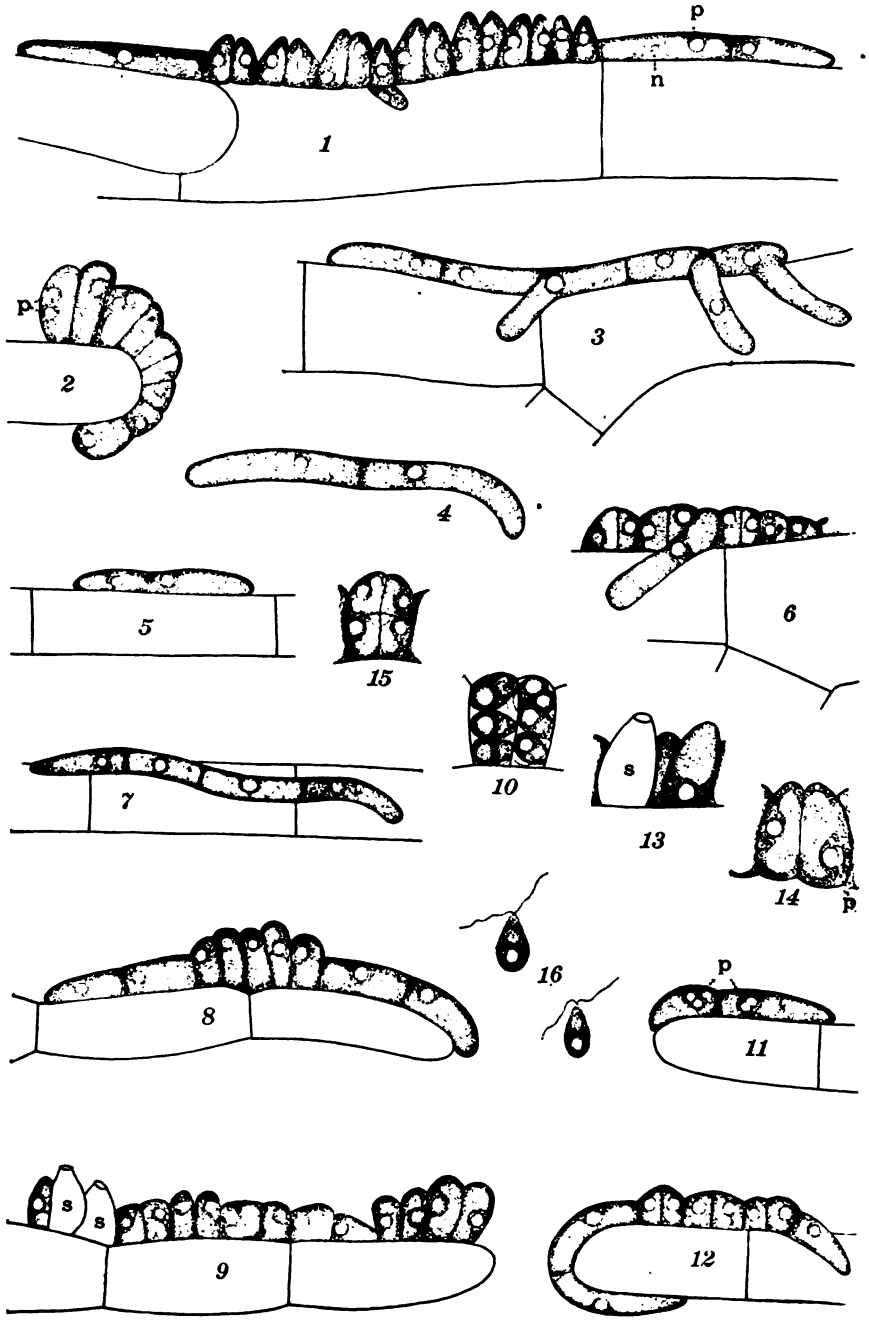

DIDYMOSPORANGIUM REPENS

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TUFTS COLLEGE STUDIES, Vol. III, No. 3.
(SCIENTIFIC SERIES.)

TWO NEW SPECIES OF STIGONEMA.

By FRANK N. BLANCHARD.

PUBLISHED BY THE CHARLES HYDE OLMSTEAD FUND.

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TUFTS COLLEGE STUDIES, Vol. III, No. 3.

TWO NEW SPECIES OF STIGONEMA.[1]

FRANK N. BLANCHARD.

(Plate 105.)

IN some material collected in October, 1909, by Dr. F. D. Lambert of Tufts College, from Chebacco Pond in the town of Essex, Essex County, Massachusetts, there was found very abundantly a blue-green alga, that apparently had not been described before, belonging to the family *Stigonemaceae.* This material was put into formalin and left until November, 1912, when Dr. Lambert and myself secured fresh material from the same place and found the same alga still plentiful. In April, 1913, I visited the pond and found the alga very scarce, but in exactly the same growing condition as in the previous November. It was found free-floating among other algae, chiefly blue-greens, where dead leaves and stems had collected in masses at the edge of the pond. Its filaments form loose, wiry-looking clusters from one to several millimeters in diameter.

The plant in the vegetative condition consists of blue-green filaments, 20–36 microns wide, that are repeatedly branched in every direction. Occasionally three or four branches may arise from adjacent cells, but the branches are usually more scattered. Although it is usually true that a branch is narrower than the filament it comes from, it may be equal to it in width, but never greater. In all the material collected the majority of branches appeared to be developed for the sole purpose of forming hormogones. No free vegetative ends of filaments, that were not forming or that had not already formed hormogones, were observed in all the material examined. The filaments are usually composed of a single row of cells, but two cells very frequently occur side by side. The colorless connections between the cells are plainly shown in formalin preserved material (fig. 8).

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[1] Contributions from the Biological Laboratories of Tufts College, No. 55. Reprinted from *Rhodora*, vol. 15, pp. 192–200, Plate 105, November 1913.

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Lateral heterocysts are common (fig. 3). Intercalary heterocysts often occur just below a hormogone, and sometimes in other places, but they are less common than the lateral heterocysts. They contain no granules and vary in color from a light brown to a very dark blue.

The sheath is usually colorless, but many times is tinged at the ends of branches with a light, golden brown. The sheath varies from four to eight microns in thickness.

Filaments grow in length and develop branches by simple division of cells. Early stages in formation of a branch are shown in figures 1, 2, and 3. Hormogones are found of all lengths up to 196 microns, and their width is the same as that of the vegetative cells. They are developed in special branches and at the ends of main branches; they may occupy the whole of a branch and project down into the main filament, or may occupy only a part of the branch (figs. 3 and 6). When the plant is most actively forming hormogones, the vegetative cells become more and more vacuolated (figs. 1, 2, 3, and 6), and after the hormogones have escaped, the vegetative cells, sometimes if not always, degenerate. In one plant observed, every hormogone had escaped, and the sheath and cells had become a uniform brown, showing evident degeneration after escape of hormogones. Intermediate stages in this degeneration are easy to find.

The hormogones escape by a breaking off of the end of the sheath as in figure 6, or by apparent disorganization of the end of the sheath. The actual discharge of the hormogone is a slow process and appears to be accompanied by the discharge of a mucilaginous mass (figs. 4 and 5). The hormogone may escape from the sheath as a whole or may break up into groups of one, two or more cells, either before or after leaving the sheath, as shown in figures 4, 5, and 7. In very young hormogones, the line of division between the cells is not clear, but as they grow older this line of separation increases in distinctness. The color of the hormogones changes as they mature, from the light blue-green of the vegetative cells to a very dark blue-green, which under the microscope appears almost black. This is probably due to a concentration of material. For this alga I propose the name

STIGONEMA **anomalum** sp. nov. Filis liberis, inter algas varias sparsis, repetite et irregulariter vel subsecundatim ramosis, 20–36 μ crassis; ramis patentibus, filo primario nunc aequicrassis, nunc tenuioribus, omnibus hormogoniferis; vagina 4–8 μ crassa, continua, hyalina vel ad apices aureo-fusca; cellulis diametro brevioribus, rectangularibus vel

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disciformibus, uni- vel biseriatis, aerugineis; heterocystis lateralibus, rarius intercalaribus, fuscis vel coeruleis; hormogoniis terminalibus, longitudine variis, usque ad 196 μ, aerugineis.

Filaments unattached, floating among other algae, repeatedly branched in every direction, or somewhat secundly, 20–36 μ diam.; branches patent, of the same size as the primary filament or sometimes thinner, all producing hormogones; sheath 4–8 μ thick, even, hyaline or sometimes golden brown at the apex of a branch; cells shorter than their diameter, mostly disciform or rectangular, of one or two series of cells, blue green; heterocysts lateral, less commonly intercalary, from brownish to blue-green; hormogonia terminal, of varying length, up to 196 μ.

Forming loose clumps, free floating among other, mostly blue-green, algae, Chebacco Pond, Essex, Massachusetts.

S. anomalum is a typical *Stigonema* for the following reasons: It is composed of one or two rows of cells; it is repeatedly branched in every direction; all branches bear hormogones; the cells are usually shorter than wide; the sheath is sometimes colored a light brown. It is allied to *Fischerella* and *Hapalosiphon* by its tendency to unilateral branching; by its smooth sheath; by the first cell of a branch projecting into the main filament; and by its generally rectangular cells.

Stigonema ocellatum is the only plant that could be confused with *S. anomalum*. I examined the specimen labeled *S. ocellatum* collected by G. T. Moore, in 1897 and distributed in Collins, Holden & Setchell, Phyc. Bor.-Am., No. 455, and concluded that my plant was not a new one after all, as it agreed very closely with Moore's plant. I then examined, through the kindness of Mr. Charles Bullard, the specimen of *S. ocellatum* from the Farlow Herbarium, originally from the herbarium of Bornet and Thuret, and decided that Moore had wrongly identified the plant he sent out, and that he had distributed *S. anomalum* under the name of *S. ocellatum*. *S. anomalum* has main filaments of about the size of *S. ocellatum;* as in that species, they consist usually of a single series of cells, occasionally two cells being side by side; otherwise, there is little resemblance. *S. anomalum* differs from *S. ocellatum* in the following ways:

1st. The wall is not very thick; the outline is straight, not following the individual cells.

2nd. There is no lamination either of the general wall, or about the individual cells. This latter, annular lamination, is what gives *S. ocellatum* its specific name.

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3rd. The wall is usually colorless; in *S. ocellatum* it is generally colored, sometimes very strongly.

4th. In *S. anomalum* the cells are not rounded, but are mostly disciform.

5th. The branching is repeated, usually with diminution of diameter.

6th. The hormogones are generally longer than in *S. ocellatum.*

7th. The way the branches arise in *S. anomalum* is rather of the *Hapalosiphon* type, the one or two cells in the main filament appearing to belong to the branch rather than to the main filament.

Specimens of *Stigonema anomalum* will be distributed in the Phycotheca Boreali-Americana; the material was preserved in formalin before it was dried, and somewhat shrunken specimens are the result.

In the material collected in 1909, as above described under *Stigonema anomalum,* there was also found a new species of *Hapalosiphon.* Although there is no doubt that it is a *Hapalosiphon,* yet it is even more an intergrading form between *Hapalosiphon* and *Stigonema* than is *S. anomalum.* It was found free-floating under the same conditions as *S. anomalum,* but in appearance it is a small, soft sod a few millimeters across, of a blue-green to brownish color.

In the vegetative condition the plant consists of blue-green or brownish filaments from eight to sixteen microns wide that are repeatedly branched in every direction. There is a tendency for the branching to be unilateral as in *S. anomalum,* and for the secondary branches to be less in number than the primary branches. The branches do not taper toward the extremities, but are sometimes slightly clavate. The branches may or may not be slightly narrower than the primary filament. The cells are nearly always disposed in a single row. The exception shown in figure 9 is rare. All the figures of this plant were made from material preserved in formalin and although there is very little shrinkage, yet there is just enough to show, in many places, the colorless connections between the cells. The cells are mostly cylindrical, usually longer than wide, and closely packed in the sheath. The colorless intercalary heterocysts are common (fig. 10). The sheath is mostly smooth, always colorless, and from two to four microns in thickness. At the ends of hormogone-bearing branches, the sheath is often thickened up to twelve microns (fig. 12). The cells of the branches are sometimes longer than those in the main filament, but are often shorter.

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Filaments grow in length and develop branches by simple division of cells as shown in figure 9. Hormogones 37–163 microns in length and 8–12 microns in width occur at the ends of all branches or in short special branches. The cells of the hormogones are not well marked off from each other. Their color remains blue-green throughout their growth. The short hormogone-bearing branches are all variously curved (fig. 10).

STIGONEMA **medium** sp. nov. Filis liberis, inter algas varias sparsis, repetite et irregulariter vel subsecundatim ramosis, 8–16 μ crassis; ramis patentibus, filo primario plerumque tenuioribus, cylindricis vel clavatis; vagina 4–8 μ crassa, ad apices usque ad 12 μ, continua, hyalina; cellulis plerumque diametro longioribus, cylindricis, uniseriatis, aerugineis vel fuscis; heterocystis forma et magnitudine cellulis normalibus similibus, hyalinis, intercalaribus; hormogoniis terminalibus, 37–163 $\times$ 8–12 μ, aerugineis.

Filaments unattached, floating among other algae, repeatedly branched in all directions or somewhat secundly, 8–16 μ diam.; branches patent, generally thinner than the primary filament, cylindrical or clavate; sheath 4–8 μ thick, up to 12 μ at the ends of the branches, even, hyaline; cells usually longer than their diameter, cylindrical, in one series, blue-green or brownish; heterocysts similar to ordinary cells in form and size, hyaline, intercalary; hormogonia terminal, 37–163 $\times$ 8–12 μ, blue-green.

Forming a minute, soft sod, among other algae, mostly blue-green, Chebacco Pond, Essex, Massachusetts, October, 1909.

This plant shows characteristics of both *Hapalosiphon* and *Stigonema*. It is characteristically a *Hapalosiphon* from its single row of cylindrical cells usually longer than broad; from its method of branching, and in that it usually has the cells in the branches longer than those in the main filament. It has the characteristics of a *Stigonema* in its habit of forming hormogones in the apices of the branches; in the fact that in many of the branches the cells are no longer than those of the main filament or are shorter; in its secondary branching, and in its branching not being distinctly unilateral.

The genera *Hapalosiphon, Stigonema,* and *Fischerella* are in many respects alike. In the table on the next page their chief characteristics may be compared at a glance. This table gives a little more latitude than some of the best writers allow; O. Kirchner, for instance, does not admit secondary branching in *Hapalosiphon*. Different accounts of the same species in these genera often vary greatly, but a safe ground has been taken in compiling this table.

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It will be seen from this summary that these genera are separated from each other by no clear and definite lines. There are several intergrading forms. The characters that are used to distinguish them are as follows:

Hapalosiphon grows free-floating in fresh water.

Fischerella grows in moist earth, on wet stones, and in hot springs.

Stigonema grows free-floating or on wet stones.

Stigonema is usually much wider than either of the other two; is often composed of several rows of cells, and the cells are usually more rounded than in *Hapalosiphon*.

The branches in *Fischerella* come from a creeping main filament and are unilateral. In *Hapalosiphon*, the branching is unilateral and secondary branching is relatively uncommon, while in *Stigonema* the filaments may be repeatedly branched in every direction. In contrast to *Stigonema*, *Hapalosiphon* has the cells of its branches longer than those of the main filament. A brown or black sheath is characteristic of *Stigonema*, but some of its species have a colorless sheath.

The question now is whether these differences are sufficient to separate three genera, especially after considering the characteristics of the two new plants above described. Bornet and Flahault in "Revision des Nostocacées Hétérocystées," 1887, class those forms now known as *Stigonema* under the subgenus *Sirosiphon*, and treat *Fischerella* as another subgenus of the genus *Stigonema*. Later, 1895, Gomont proposed raising *Fischerella* to the rank of genus, basing his proposal "sur la différenciation très marquée des filaments primaires rampants, relativement aux filaments dressés." West, in "British Fresh Water Algae" considers *Fischerella* to belong with *Hapalosiphon*.

Thus, there has already been considerable difference of opinion as to the relationship of these forms. *Stigonema anomalum* shows similarity to *Hapalosiphon* in that its cells are commonly nearly rectangular; its sheath is smooth; there is a distinct tendency to unilateral branching; and the first cell of a branch usually projects into the main filament as in *Hapalosiphon*. *S. medium* shows itself distinctly like a *Stigonema* in its repeated branching; in the fact that the branches do not taper in the least and are often slightly clavate; and in the fact that hormogones are formed in abundance in all the branches. It also differs from the *Hapalosiphon* in having the cells of the branches often shorter than those of the main filament. It therefore seems necessary

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	Reproduction	Width of Filament	Length of Hormogones	Number of rows in Filaments	Style of Branching	Sheath	Cells	Heterocysts
Hapalosiphon	Hormogones and spores; chiefly spores	4 to 24 microns	All lengths	One, rarely two	Chiefly unilateral; secondary branching relatively uncommon	Smooth; colorless	Generally rectangular	Intercalary
Fischerella	Hormogones and spores	6 to 13 microns	Very long	One or two	Unilateral; branches from creeping main filament; no secondary branching	Smooth; colorless	Rectangular, or rounded	Intercalary
Stigonema	Hormogones and spores; chiefly hormogones	7 to 90 microns	All lengths	One, two, or more	In every direction; frequent secondary branching	Smooth or rough; colorless or brown to black	Rounded; less commonly rectangular	Intercalary or lateral

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to put these three genera together as subgenera of the genus *Stigonema*, and let *Sirosiphon* be the subgenus comprising those forms now known as *Stigonema*. Thus:—

Genus, Stigonema Agardh.

1. Subgenus Sirosiphon Bornet & Flahault.
2. Subgenus **Hapalosiphon** (Nägeli) subg. nov.
   Nägeli ex Bornet & Flahault, Revision des Nostocacées Heterocystées, part 3, p. 54, 1887, as genus.
3. Subgenus Fischerella Bornet & Flahault.

Acknowledgement is due to Mr. Frank S. Collins for loan of books and assistance by suggestion, to Mr. Charles Bullard for loan of herbarium specimens, and to Dr. F. D. Lambert for material and assistance.

BIBLIOGRAPHY.

Bornet and Flahault: Revision des Nostocacées Heterocystées; part 3: 1887.
West, G. S.: British Freshwater Algae, Cambridge, 1904.
Kirchner, O., in Engler and Prantl, Naturliche Pflanzenfamilien, Teil 1. Abt. 1a, 1898.
Tilden: Minnesota Algae, vol. I, 1910.
Wolle: Fresh Water Algae of the United States, 1887.
Wood: A contribution to the history of the Fresh Water Algae of N. A., 1872.
Forti: Sylloge Myxophycearum, 1907.

EXPLANATION OF PLATE 105.

Magnification: Figures 1 to 8, × 280; 9 to 12, × 420.

Figures 1 to 8 inclusive are *Stigonema anomalum*.

Fig. 1. The beginning of a branch.
" 2. Young branch and intercalary heterocyst.
" 3. Primary filament with short hormogone-bearing branches, unilaterally arranged. Lateral heterocysts and vacuolated cells.
" 4. Escaping hormogones.
" 5. Escaping hormogone.
" 6. A branch after escape of hormogone.
" 7. Hormogones.
" 8. Formalin material showing connections between cells.

Figures 9 to 12 inclusive are *Stigonema medium*.

Fig. 9. Shows that branching is not unilateral; young branch; division of a cell; two cells side by side.
" 10. Hormogone-bearing branch, and heterocyst.
" 11. Escaping hormogone.
" 12. Thickened portion of sheath at end of hormogone.

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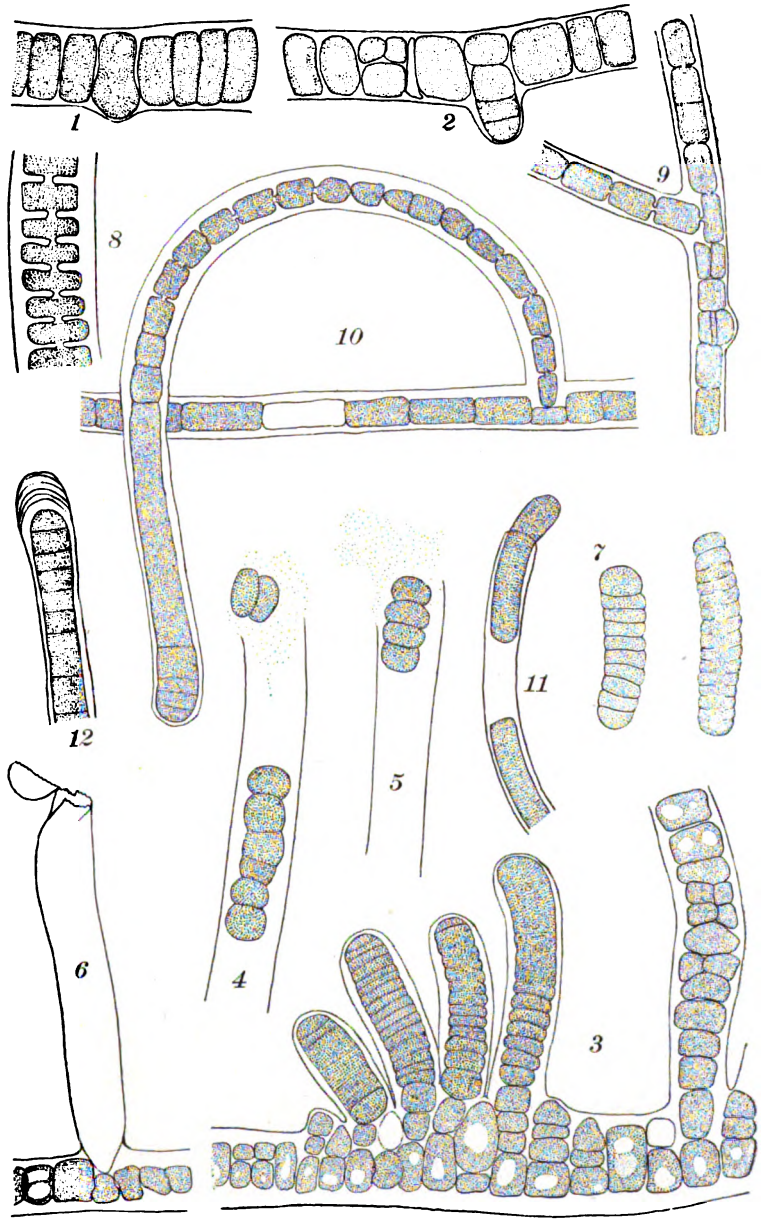

Figs. 1–8. STIGONEMA ANOMALUM Blanchard, sp. nov.
Figs. 9–12. STIGONEMA MEDIUM Blanchard, sp. nov.

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(SCIENTIFIC SERIES.)

THE MORPHOLOGY OF THE EYE-MUSCLE NERVES.

By H. V. NEAL.

(Reprinted without change of paging from the *Journal of Morphology*, Vol. 25, No. 1.)

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THE MORPHOLOGY OF THE EYE MUSCLE NERVES

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NINE PLATES AND FOUR TEXT FIGURES

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INTRODUCTION

An advocate of the orthodox view of the vertebrate head as a structure derived from segmented pre-vertebrate ancestors is likely to meet with an incredulity or an indifference quite unknown to morphologists of the last generation. The reasons for this are several. In the first place special creation has rested its case and evolution no longer feels the urgent necessity of strengthening the argument that the vertebrate head or any other organic structure has had a past history. In view of the general acceptance of the verdict in favor of evolution it appears to be a matter of minor importance just what this history has been, whether annelid, tunicate, arachnid or what-not.

Furthermore, the conflict with accumulating evidence and the disagreement in opinion among vertebrate morphologists; the divergence in results based upon the study of the ontogenesis of different vertebrates; the increasing conviction of the plasticity and mutability of ontogenesis; doubt regarding the actual specificity of the germ layers; all have tended to undermine the faith of our scientific forebears in the validity of the fundamental law of biogenesis except in its most general features. Faith in phylogenetic inductions based largely on embryological data has been greatly weakened. A distinguished embryologist (McMurrich '12) recently expressed the opinion that "more reliable results are to be obtained in the majority of cases from comparative anatomy." We must concede that the results of embryological investigation have disappointed those who anticipated general agreement regarding the phylogenesis of the vertebrate head.

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Civil war in the camp of the morphologists between anatomists and embryologists has led some to exclaim, "a plague on both your houses!" Morphology is the loser when embryologists and anatomists attack each other instead of morphological problems. The pot has called the kettle black and the luster of neither has increased. There seems to be no particular advantage in discussing the question whether comparative anatomy or embryology has been able to make the more valuable contribution to the solution of morphological problems. It appears not unreasonable to think that, notwithstanding frequent divergence of theoretical conclusions, the key to the solution of morphological problems lies in the hand of neither alone. The two sciences must develop together. The results by one method need to be 'controlled' by the other.

The elaboration of other than the annelid theory of vertebrate ancestry upon which the orthodox conception has been largely based, has tended to throw doubt upon the view that the segmentation of the vertebrate head is an ancestral segmentation. A morphologist of the last generation might have thought it necessary to apologize for advocating the view that the vertebrate head is an unsegmented portion of an unsegmented ancestor. No apology would be required today. As a matter of fact, after a century of vertebrate morphology, we actually do not know whether vertebrates came from a segmented or an unsegmented ancestor; whether or not the present segmentation in the head region is a true metamerism; whether the pre-otic portion of the head is a coenogenetic addition to a primarily segmented body, or a palingenetic remnant of an unsegmented ancestor which has secondarily acquired a segmented trunk. Even among those who agree that the present segmentation is ancestral there is little accord as to the nature or number of these somites.

A grouping of morphological opinion, however, with reference to the extremes of expression shows a strong tendency on the part of morphologists to regard the head as metameric. The curve of variation in opinion is decidedly skew in the direction of morphological orthodoxy. Among the many papers dealing

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directly or indirectly with the problem of the morphology of the vertebrate head since the opening of the twentieth century, that of McMurrich ('12) is the only one adverse to the view that the head was primitively metameric. Vertebrate morphology, however, is deeply indebted to the skeptical but stimulating spirit which has constantly compelled orthodox opinion to reestablish its fundamental tenets.

To a considerable degree the skepticism regarding the comparability of head and trunk metameres may be traced back to the demonstration of the differences between cranial and spinal nerves, the serial homology of which seemed unquestionable to the earlier morphologists. The discoveries in the field of nerve components and of their various central and peripheral relationships seemed to many greatly to increase the difficulty of comparing the nerves of head and trunk. In consequence more stress came to be laid upon longitudinal columns in the central nervous system than upon a hypothetical primitive metamerism or neuromerism.

Nevertheless, the theory of the primitive metamerism of the head is "noch nicht aus dem Welt geschafft." The last decade has not seen a diminution in the numbers of those undertaking a reinvestigation of this perennial problem, notwithstanding the attractive fields in other departments of biology which have opened up during the period. With whatever incredulity or indifference schemes of head segmentation may meet as they appear, there are indications that students of head morphology are reaching an agreement with regard to the fundamentals of the metamerism of the head. The reinvestigation of many ontogenetic and histogenetic problems, concerning which earlier investigations had led to divergent results, have led to a remarkable agreement in conclusions and have tended to remove the prejudice against ontogenetic foundations for phylogenetic conclusions. It is now seen that much of the divergence in results of earlier embryological research was the result of inadequate methods or materials—of generalizations based upon insufficient data. There is good reason for thinking that further investigation of nerve histogenesis will show a similarity between

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cranial and spinal nerves which had been rendered doubtful by the incomplete researches of earlier students of nerve development. The recent elaborate studies of the histogenesis of the trochlear and oculomotor nerves by Dohrn ('07) and Gast ('09) have tended greatly to strengthen the conviction of morphologists that these nerves are comparable with spinal nerves. Belogolowy's ('10) careful monograph on the cranial nerves of the chick leads to the same conclusion. It is the purpose of the present study to make a contribution to the same end.

The writer takes pleasure in expressing his appreciation of the aid given him during the prosecution of this research by Professor John Sterling Kingsley, Director of the Harpswell Laboratory, during the summers of 1906–1913 and for the unlimited supply of embryos of Squalus acanthias which residence at this laboratory has rendered available. He also acknowledges gratefully a grant of $50 by the trustees of the Elizabeth Thompson Fund, used in the attempt to get embryos of stages between 50 and 100 mm., not obtainable off the Maine coast during the summer months.

1. The importance of the eye-muscle nerves as criteria of the metamerism of the head

In a recent paper dealing with the head problem Ziegler ('08, p. 674) writes that, since he holds that the eye muscles are relatively young muscles which have not arisen directly from segmental muscles, he is of the opinion that one cannot make use of their innervation for phylogenetic conclusions. Ziegler does not give his reasons for regarding the eye muscles as relatively young muscles. Moreover, he does not prove that they have not arisen directly from segmental muscles, and in drawing conclusions concerning the phylogenesis of the head he makes use of the relations of the oculomotor as an essential connecting link.

Cole ('98, p. 237) also refers to the eye-muscle nerves as the "the least primitive of the cranial nerves" without giving any proof of the assumption.

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On the other hand, Gast ('09, p. 423) asserts that the eye-muscle nerves appear very conservative in their relations to the neuromeres, notwithstanding the considerable dislocation of their muscles. He therefore concludes that the eye-muscle nerves supply most important material for the study of the primitive metamerism. However profound the changes in their terminal-organs, the central relations remain unchanged, so that they serve as important criteria of the nature and number of pre-otic segments. "Die drei Augenmuskeln Nerven haben eine hohe phylogenetische Bedeutung." The writer would emphasize their importance even more than Gast has done, for it seems to him that the demonstration of the serial homology of head and trunk metameres depends largely upon the proof of the resemblance of eye-muscle and spinal somatic motor nerves.

The reason for such an opinion is plain when we consider that other evidences of cephalic segmentation, such as cranial ganglionic nerves and visceral arches, appear limited to the head region and to have no exact homologues in the trunk. The presumption that head and trunk were primarily undifferentiated must come not from such evidence but from structures which may be more readily compared. The eye-muscle nerves in connecting somites and neuromeres, are related to structures which extend through head and trunk. Moreover, in their central relations the eye-muscle nerves resemble spinal somatic motor nerves. Therefore, failure to convince morphologists of their meristic homology with spinal nerves would tend to undermine the foundation of the traditional conception of the head.

Consequently, the divergence of opinion regarding their true nature, as evinced by their ontogenesis in Selachians, has tended to obscure the more important issue of the history of the head. The repeated attempts to compare the trochlear and oculomotor with such nerves as the trigeminal and the facial, notwithstanding their obvious differences in the adult animal, suggests the necessity of renewed investigation of their histogenesis. Recent exhaustive papers by Dohrn ('07) and Gast ('09) have appeared in response to this need. In many matters of fundamental importance this paper confirms their results. The theoretical

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conclusions are not so fully in accord, but all agree that the ancestral vertebrate was a metameric acraniote, and there is no suggestion that the meristic elements of the head have had an exogenous source.

2. *Technical methods*

Considerable investigation upon the histogenesis of nervous structures has been made upon material prepared by methods unsuited to the special requirements of neurological investigation. To this may be attributed many of the fallacious inferences that have delayed our knowledge of the true method of nervous differentiation. Failure to use suitable neurological methods is no longer excusable, however, since the advances made by Cajal, Paton, Held and others. It is necessary for one who attempts today to base morphological conclusions upon the study of nerve histogenesis, to make sure by proper technique that he is dealing with real nervous structures and not with pseudo-nerves. Not every cellular strand or spindle-shaped cell, however closely associated with the central nervous system or its derivatives, is necessarily a nervous anlage. Some criterion by which a structure in the embryo may be identified as nervous is needed. Hence the importance of stains which will differentiate the neurofibrils from the time of their first appearance.

Equally important in addition, is the use of a method which will demonstrate cell boundaries and relations, especially in those early stages when nervous connections between nerve center and end-organ are established. Since no single method is known which will effect both of these results with equal precision, different methods for comparison and control of results appear necessary. Trust in a single neurological method, however highly perfected, may mislead as much as a less specific stain has done. The importance of methods of preservation and staining is evinced by the great divergence in the results, both technical and theoretical, of Paton ('07) and Held ('09), each of whom worked with a highly perfected technique.

Therefore, while it may be granted that the older embryological methods are no longer adequate for the purposes of neu-

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rological investigation, the results by no single neurological stain, however specific, may be wholly trusted. The methods suited to demonstrate the neurofibrils in vertebrate embryos give very unsatisfactory pictures of cell boundaries and relationships. But, as a basis for theoretical conclusions, the cellular relationships are quite as important as phases of differentiation of neurofibrils. Moreover, it must not be forgotten in the enthusiasm created by the newer discoveries that, provided embryological material be abundant, the identification of an embryonic structure as nervous may be determined by tracing its fate through successive stages of development. The demonstration of neurofibrillae therefore is not absolutely indispensable in the determination of its nervous character.

In the course of the present study different methods have been used. Among those which have given the best results are Cajal's nitrate of silver, Paton's modification of Bielchowsky's method, Held's molybdic acid—hematoxylin stain and vom Rath's picro-acetic-osmic-platinic chloride—pyrogallic acid treatment. All the drawings in plates 1 to 8 of this paper were made from preparations by the latter method. They have been confirmed by observations upon material in which the neurofibrillae were specifically stained.

The Vom Rath ('95) method is as follows:

1. Fix in the dark for one to three days in the following mixture (use plenty and change each day):

Saturated and filtered solution picric acid	200 cc.
Glacial acetic acid	2 cc.
Platinic chloride (dissolve in 10 cc. water)	1 gram
Osmic acid 2 per cent	25 cc.

Owing to the great brittleness of embryos fixed in this fluid all changes of liquid should be made with pipette in the same dish, avoiding as far as possible any movement of the embryos.

2. Stain in 0.5 per cent pyrogallic acid in the dark for twenty-four to forty-eight hours with several changes.

3. Grades of alcohol from 35 per cent slowly by the siphon capillary drop method to avoid shrinkage. Xylol, to which paraffin is added as it dissolves.

4. Imbed in rather hard paraffin of best quality.

5. Thin sections, not over 8 micra, preferably 4 to 6 micra.

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Vom Rath's method is not specific for the neurofibrils, which are nevertheless deeply stained. Cell boundaries are shown with special distinctness and shrinkage is slight. The process is advantageous in demonstrating cell relations in the stages when nervous connections of tube and somite are effected.

Flemming's stronger formula gives excellent fixation of selachian embryos but does not allow the use of pyrogallic acid for subsequent staining. Fixation seems quite as faithful as in Vom Rath preparations, but cell boundaries are not so distinct as in the latter. Iron hematoxylin gives the best stain, subsequent to the use of Flemming's fluid, but it is necessary to paint the sections with 0.5 per cent celloidin in order to prevent their loss in staining on the slide.

For the specific purpose of demonstrating the neurofibrils Cajal's method has given uniformly satisfactory results, which appear somewhat less refined than those obtained by the Bielchowsky-Paton process. The Cajal method is as follows:

1. Fix in absolute alcohol and 1 per cent ammonia for forty-eight hours.
2. Wash for one-half to three minutes in distilled water.
3. Pyridine for twenty-four hours.
4. Distilled water—many changes—for twenty-four hours.
5. Two per cent aqueous solution of silver nitrate for three days at 35°C. in the dark.
6. Rinse in distilled water.
7. Four per cent pyrogallic acid in 5 per cent formalin for one to two days.
8. Paraffin sections.

The Simarro-Cajal silver reduction method, following fixation in 70 per cent pyridin, which has given such splendid results when applied to mammal and other amniote embryos has proved a complete failure in the case of Squalus embryos.

Excellent results in the differentiation of the neurofibrils have followed the use of the molybdic-acid hematoxylin process as developed by Held ('09). Tissues may be fixed by various methods including Zenker's fluid and Rabl's picro-sublimate. The stain is effected by a solution of molybdic acid in a 1 per cent solution of hematoxylin in 70 per cent alcohol. The stain

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is better after months or years. Immediately before use, several drops of this tincture—depending on the strength wanted—are dissolved in distilled water and the sections are stained warm on the slide at 50° C., or for a longer time cold. The sections may be stained directly or they may be mordanted in iron alum.

The neurofibrils are differentiated by the Bielchowsky-Paton process but, like the Cajal method, this does not demonstrate the fibrils within the neuroblast cell in the earliest stages of histogenesis. By this method the neurofibrils are stained a dark brown or black, while other tissues are light brown or yellowish brown. In the process only tested distilled water and absolutely clean glass ware and glass or bone spatulas—no metal—should be used:

1. Fix and keep embryos in 10 per cent formalin neutralized or made slightly alkaline with magnesium carbonate.
2. Wash in running tap-water for twelve hours.
3. Wash in three or four changes of distilled water for a half-hour.
4. Place in pure 1 per cent nitrate of silver for six days in the dark at a temperature of about 70°C. Tissues must become reddish-brown in color. If they become yellowish-brown, throw away.
5. Place in a solution of silver nitrate freshly prepared as follows: 20 cc. of 1 per cent silver nitrate. Add 2 drops of 40 per cent caustic soda to form a gray precipitate. Then add 20 to 30 drops of strong ammonia, enough to dissolve the precipitate while stirring. Allow to remain at least forty-five minutes.
6. Wash quickly in two baths of distilled water and quickly place in distilled water, to every 20 cc. of which five drops of glacial acetic acid has been added. Leave in this five to fifteen minutes or until the reddish-brown becomes yellowish brown.
7. Wash quickly and place over night in 1 per cent hydroquinone containing 5 per cent neutral formol.
8. Wash quickly in distilled water, run up through alcohols rapidly and imbed in paraffin through benzole or chloroform.
9. Cut sections and fix on slide. Dry well, then paint slides with 0.5 per cent celloidin. This is followed by absolute alcohol-xylol, and absolute alcohol-xylol again. Then absolute alcohol to 95 per cent alcohol down to water (distilled).
10. Then one to two hours in 0.1 per cent solution of gold chloride neutralized with lithium carbonate. Grubler and Hollborn's gold chloride should be used (flavum, not fuscum).
11. Rinse in distilled water and fix in 5 per cent hyposulphite of soda for fifteen minutes. Wash in running tap water for two hours. Then alcohols up to absolute. Then absolute and eosin for a minute. Absolute alcohol, xylol, and mount in neutral balsam.

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HISTOGENESIS OF SPINAL SOMATIC MOTOR NERVES

1. General description

Somatic motor nerves make their first appearance in embryos of Squalus acanthias of about 4.5 mm. and approximately 30 somites. With their advent begins the rhythmical bending of the embryo. The first pair of somatic motor nerves to appear are those of VanWijhe's seventh somites, the first somites differentiated, and those which form the first permanent myotomes.

Previous to the appearance of this first pair of somatic motor nerve anlagen, no protoplasmic connections or plasmodesms between tube and somite are discernible. In the intercellular space between neural tube and somite there is present a plasmoid substance or a liquid with a minimal amount of coagulable material, which, when treated by the usual reagents, assumes a vacuolated appearance. By the use of such fixing fluids as neutral 10 per cent formalin, followed by intense stains such as acid fuchsin it is possible to demonstrate this coagulable substance with considerable clearness. By the use of other fixing fluids—the plasmolyzing action of which is less intense than that of formalin—and the use of less powerful stains, the plasmoid material is almost invisible and has usually been ignored in embryological studies. Whatever may be the chemical nature of the granules of this plasmoid substance, it does not have the staining properties of protoplasm and its presence may not therefore be taken as evidence of a primary protoplasmic connection between tube and somite, although it is indisputably the medium through which the growing nerve anlagen find their way to the adjacent myotomes.

While the possibility that this plasmoid material may contribute to the growth of the nerve paths may not be denied, yet even so the contribution must be very slight or quite negligible, since the amount of coagulable material in it is very small. To represent it at all, as in figure 1, greatly exaggerates its distinctness and amount as seen in sections. There is nothing in its vacuolated structure that would suggest 'paths' or 'plasmodesms' suggested by the Hensen hypothesis. Moreover, the

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proximity of tube and somite is so close that the absence of predetermined paths for the growing nerve is not surprising. Supporters of the Hensen hypothesis have greatly exaggerated the mechanical difficulty of the acquisition of a connection between tube and myotome in the absence of primary paths. But even the most ardent supporter of the Hensen hypothesis will admit the capacity of cells to throw out amoeboid processes into the surrounding medium, and for distances quite as great as that which separates somite and neural tube.

As a matter of fact, protoplasmic connection between tube and somite to form the anlagen of somatic motor nerves in Squalus is effected in precisely that way, as was described by Dohrn ('88) many years ago. The process is one of amoeboid outflow, as stated by that accurate observer, and as shown in figures 4 to 7 of this paper. Beginning with the seventh somite of the selachian embryo protoplasmic connection with each of the successive somites of the body is effected in the same way, that is, by amoeboid processes of medullary cells of the ventrolateral wall of the neural tube opposite the middle of the somites. Since the successive somatic motor nerve anlagen are successively formed, beginning with the most anterior, all stages in the establishment of these connections of nerve and muscle may be seen in serial cross-sections of Squalus embryos of all stages beginning with embryos of 30 somites. The process goes on in the caudal region until quite late stages are reached.

The protoplasmic connections which form the anlagen of somatic motor nerves are not formed by the differentiation of plasmodesms which have existed from the beginning as the result of incomplete cell division, but are formed secondarily by the free outgrowth of amoeboid processes of medullary neuroblasts. The process is one of protoplasmic movement, analogous to that seen in the remarkable culture preparations of Harrison and to the outgrowth of the neuraxons of the Rohon-Beard cells illustrated in plates 3 and 4 of this paper. Stages in the establishment of these connections between tube and myotome and in the growth of the nerve anlagen are shown in plates 1 and 2 of this paper.

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In correlation with this movement of medullary protoplasm there occurs a similar movement of the protoplasm of the cells of the sclerotomic portion of the somite, which is inaugurated by an extension of amoeboid processes toward the neural tube (figs. 2 and 3) followed in later stages by a movement of entire cell bodies. In many cases, but not invariably, the movement of the sclerotome cells precedes that of the medullary cells. The protoplasmic material derived from the two sources in exceptional cases unites to form a protoplasmic strand or plasmodesm in which it is difficult to distinguish ectodermal and mesodermal constituents, as is shown in figures 8 and 9. This difficulty obtains, however, only in the earliest stages, if it occurs at all. Even in such cases the sclerotome cells soon separate to form a loose mesenchyma of lightly staining and much vacuolated cells, while the medullary portion persists as a compact strand of deeply staining protoplasm which quickly takes on a fibrillar appearance and also becomes cellular through a process of cellular migration from the neural tube (figs. 11 and 12).

Evidence that the cells of the somatic motor nerve anlagen of Squalus are chiefly, if not exclusively, of medullary origin has been given in an earlier paper (Neal '03) and need not be reviewed in detail at this time. Their medullary derivation seems sufficiently attested by evidence of continued migration in successive stages; by their close apposition to the fibrillar bundle or their inclusion within the fibrillar portion of the nerve anlage (fig. 12); by the change in the contour of the neural tube in successive stages as seen in cross-sections; and by the relations of the outer limiting membrane of the tube to the nerve anlage. If mesenchymatous cells are added to the nerve anlage at all, it appears to be in later stages of histogenesis only.

While spinal somatic motor nerve anlagen are primarily protoplasmic and non-fibrillar this stage is quickly passed and, as the anlage extends ventrad along the median surface of the myotome between the myotome and sclerotome of the somite, it assumes a fibrillar appearance. That these fibrils are neurofibrillar in the Apathy sense is proven by the fact that they stain intensely in either Cajal or Baton preparations. Evidence

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has been given in an earlier paper that the cells of the nerve anlagen have no genetic relations to the fibers. The fibers may be traced to deeply-staining bipolar neuroblasts in the ventrolateral wall of the neural tube.

When sections in metameres immediately posterior to those in which protoplasmic connections between tube and somite have just been established by the outflow of medullary protoplasm are studied; that is, in metameres in which it may be assumed that protoplasmic connections are about to be established by a similar outflow, before the medullary cells have thrown out amoeboid processes, deeply staining cells may be found which may be inferred to be the neuroblasts of that metamere. Their more deeply staining properties may be ascribed to the presence of a deeply stained neuroreticulum within them. Analogy with the histogenesis of the Rohon-Beard cells favors this inference, since within the latter, from the time of their differentiation from the surrounding epithelial cells of the tube, a reticulum with a strong affinity for stains makes its appearance and seems to be genetically related to the neurofibrillae which later make their appearance within the long processes of these remarkable cells (plates 3 and 4). In Cajal preparations similar cells in similar relations show a deeply-stained reticulum. There is therefore reason for thinking that the neurofibrillae of somatic motor nerve anlagen have their origin in medullary neuroblasts and are not exogenous in their derivation as suggested by Paton ('07). In all stages the fibers of the nerve anlagen may be traced to deeply-stained bipolar cells in the somatic motor column of the neural tube. While it is difficult to obtain positive proof of the fact, the evidence, so far as it goes, favors the opinion that the cells which form the first protoplasmic connections between tube and somite are true neuroblasts and not indifferent cells which form protoplasmic paths for the nerves, as suggested by the cell-chain hypothesis or by the similar hypothesis of the Hertwigs. In short, connections between tube and somite are effected primarily by neuroblasts and not by indifferent cells. These primary connections appear protoplasmic and not fibrillar, only because

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they are formed by the amoeboid terminations of the neuraxon processes. The protoplasmic and fibrillar relations are precisely analogous with those seen in a Rohon-Beard cell such as is represented in figure 21. The advancing end of the neuroblast cell is protoplasmic and amoeboid, while the more proximal portion of the cell has a neurofibrillar structure. There appears no good ground for doubting the analogy between the phenomena of growth of the Rohon-Beard cells and those of the medullary neuroblasts which form the fibrillar constituents of somatic motor nerves. The evidence of the exogenous derivation of the neurofibrils advanced by Paton seems unquestionably based on incompletely stained preparations. The assumption of the participation of indifferent cells in the formation of 'paths' for the growing nerve fibers has an equally insecure foundation.

After the fiber bundle of the dorsal (somatic sensory) nerve unites with that of the somatic motor nerve a cluster of cells makes its appearance median to the mixed bundle at about the level of the dorsal aorta, forming the anlage of the sympathetic ganglion. The derivation of these cells from the neural tube has sometimes been assumed. The majority of opinion has inclined to the view that they are derived from the dorsal ganglia. Positive proof of either inference has never been given on the basis of direct observation. Experimental data appear not absolutely trustworthy. The present paper makes no contribution toward the solution of this important question. Analogy with the formation of the sympathetic in the head appears to the writer to favor the view that the most of the sympathetic cells have their source in the dorsal ganglia. The problem, however, needs renewed investigation.

Turning now to a more detailed discussion of some of the mooted points in the problem of nerve histogenesis, we may take up first the important question of the primary connection between nerve and muscle.

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2. Are muscle and nerve connected with each other ab initio? Are protoplasmic connections between myotome and tube primary or secondary?

With the statement of this question we plunge at once into the most controverted point in neurogenesis—the problem of how nerves become connected with their terminal-organs. The earlier students of head morphology avoided the details of nerve histogenesis. Yet it is clear that the morphological resemblance of nerves is determined quite as much by their cellular and central connections as by the character of their terminal-organs. In the adult elasmobranch and in the higher vertebrates these relationships are frequently so greatly modified and complicated that to unravel their intricacies requires the facts which the ontogenesis of the lower vertebrates alone can give. Avoidance of the details of histogenesis and reliance upon embryological procedure unsuited to neurological investigation has led to the inclusion of cell clusters or strands among cranial nerves without proof of their nervous character and to erroneous inferences regarding the phylogenesis of the head. Minot ('96) suggested this weakness of earlier researches and the path of later investigation when he wrote that "the attempt has been made to solve the most difficult questions of the morphology of cranial nerves without answering the inconvenient question of nerve fibers and their sheaths." To-day the student of phylogenesis is no longer able to shut his eyes to the necessity of a thorough investigation of the genesis of nerves before drawing conclusions regarding the past history of the vertebrate head.

In the introduction to his masterly discussion of nerve histogenesis, Held ('09) states that notwithstanding the numerous observations of the past fifty years and the multiplicity of hypotheses, the question as to how nerves are formed in the embryos of vertebrates is one of the most burning questions of embryology:

> Many new methods have been applied to its solution and a surfeit of new views have appeared, following one another in a short period of time, but as yet no agreement has been reached regarding the true principle of nerve development. This is due to a great extent to the

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lack of a fundamental histological method which effects a satisfactory stain for embryonic as well as for adult nervous tissue. But the disagreement is also partly due to the fact that it has been the concept rather than the reality that has been observed. Finally the continued conflict of opinion has been due to the fact that no comprehensive observations have been brought together which make it possible to demonstrate in one and the same animal all of the essential stages in the development of a definite nerve path, and to extend in a comparative research over the chief groups of vertebrates, in order to find, in the diversity of phenomena seen in different embryos, the same fundamental principle of nerve development.

Held undertook this herculean task and has made a most valuable contribution to our knowledge of the histogenesis of the neurofibrillae, which, since the emphasis laid upon them by Apathy, have come to be regarded as the essential elements of the nerve fiber. In large measure Held's monograph is an attempt to reconcile the divergent hypotheses of nerve histogenesis.

Three chief theories of nerve histogenesis have been advanced. Chronologically arranged these are:

1. The theory advanced by von Baer in 1829 and later elaborated by Hensen ('64, '76, '08) of the primary connection of the nervous center with its later innervated terminal-organ. The fundamental idea underlying this von Baer-Hensen theory is that of the necessity of a primitive connection between the nerve and its terminal organ. In other words that it is impossible to conceive of a nerve fiber finding its area of distribution or its terminal-organ as the result of the free outgrowth of the nerve cell. Hensen brought forward the idea of primary nerve paths, which was founded on the actual observation that in the embryo adjacent organs are connected with each other by means of protoplasmic bridges. These were interpreted as remnants of incomplete cell divisions and they were supposed to form the primary nerve paths which later become transformed into the definitive nerves or are used for nerve formation. How the transformation occurs was unknown to Hensen, but he was convinced that they did not develop from cell outgrowths. The theory appeared to afford a satisfactory explanation of how nerves find their way to their terminal-organ. Chiefly on the ground of general principles, Gegenbaur ('98), Fürbringer ('97), Kerr

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('04) and Braus ('05) have added to the Hensen hypothesis the assumption of an original and unchangeable connection of motor nerve and muscle.

Held ('09) suggests that the assumption of primary—ab initio—connection between muscle and nerve is not an essential part of the Hensen hypothesis. With this view, however, Hensen ('03) does not seem to agree. Hensen states his hypothesis in his Vorrede as follows: "Nervous connections are not established through the free outgrowth of the nerves in the embryo, but central and peripheral organs remain in connection with each other from the time of their formation (Sonderung) until the complete differentiation of the nervous trunks."

2. The second theory is that advanced by Schwann ('39) and later revived by Balfour ('77) as the cell-chain hypothesis, according to which the nerve fiber arises from the union of a series or chain of primary cells, which later accompany the neuraxon as the so-called Schwann's or neurilemma cells. According to this hypothesis nerve fibers are formed by the fusion of primary cells, whose nuclei become the nuclei of the differentiated fiber, so that the nerve fibers are in consequence multicellular in origin. This theory has been supported by Marshall ('78), VanWijhe ('82, '86, '89), Beard ('85, '88, '92), Miss Platt ('94, '96), Sedgwick (94, with some modification), Hoffmann ('96), Kupffer ('90, '91, '94), Rafaelle ('00), Bethe ('00–'07, with modifications), Brachet ('05, '07), Cohn ('05, '06, '07), Oscar Schultze ('04–'07).

According to the cell-chain hypothesis, the peripheral nerve fiber is the common product of a chain of cells, on the end of which, in the case of a motor nerve, or in an intermediate position, in the case of a sensory nerve—the larger cell forming the ganglion cell is situated. The cell chain not only forms the ganglion cell but also the cells of the neurilemma sheath, which are not merely sheath cells but also the cells that produce the fiber—as nerve-fiber cells or 'neurocytes' (Kupffer), 'nerve-cells' (Bethe and Apathy) or 'neuroblasts' (O. Schultze). The nerve fiber is thus an elongated mosaic consisting of a series of cells, each cell of which has added to what another cell before it has formed, and has continued into the following cell. Bethe ('00–

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'07) has modified this view by assuming that mitotic cells form the first anlage of the nerve and the development of the nerve proceeds by cell multiplication. Not every fiber, however, arises from a series of cells, but a series of cells produces a large number of fibers.

3. The third theory of nerve histogenesis, first formulated by Kupffer and Bidder ('57), but finally developed as the neuroblast theory by His ('79), holds that the nerve fiber develops as the process of an embryonic ganglion cell. Even before this theory had been advanced it had been noted by Remak ('55) that nuclei are absent in embryonic nerves. His ('79, '88, '90, '93, '04) developed this process theory of Kupffer and Bidder as the 'neuroblast theory' of nerve histogenesis, according to which nerves are formed as processes of special cells or 'neuroblasts.' The first outgrowth of these cells forms the axis cylinder and the cell becomes a ganglion cell. A single process is formed by the neuroblasts of the neural tube, while two are produced by the neuroblasts of the peripheral ganglia. Other branched processes formed later become the dendrites of the ganglion cells. Thus every single nerve fiber represents a single and definite cell of origin which constitutes its genetic, nutritive and functional center. These nervous units do not unite with each other in protoplasmic continuity, but a transfer of impulses occurs without continuity. This view has been supported by von Koelliker ('86, '91, '92, '00, '05), Sagemehl ('82), Ramón y Cajal ('90–'07), von Lenhossek ('90–'03), Retzius ('93), Neal ('98, '03, '12), Gurwitsch ('00), Harrison ('01–'12), Bardeen ('03), Lewis ('06, '07), Dohrn ('07), Belogolowy ('10) and Burrows ('11).

Waldeyer ('91) has still further developed the neuroblast theory as the neuron theory, according to which the nervous system, both central and peripheral, consists of independent functional units—cells or neurons—which never become fused or united but transmit impulses by transfer or induction from one neuron to another.

Later investigators have advocated various modifications of these three theories, but not hypotheses that may be sharply distinguished from the three theories mentioned above. They

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may be regarded as variations of a theme rather than as original themes. The brothers Hertwig, for example, on the basis of evidence derived from the study of the development of nerves in medusae, suggested ('78) the hypothesis that the terminal organ, primarily separated from the nerve center, becomes secondarily connected with it by means of a simple protoplasmic path which is later differentiated into the actual nerve. The connection between nerve center and terminal-organ is formed secondarily, is at first protoplasmic and not nervous, and is the product of indifferent cells and not those which form the nerve fibers. Such protoplasmic connections become the paths along which the nerves develop and are established when nerve center and terminal-organ are in close proximity. This hypothesis, in common with that of Hensen, lays stress upon the protoplasmic paths within which the definite nerve fibers are differentiated, but differs from the Hensen hypothesis in assuming the secondary connection between center and terminal-organ. The hypothesis, however, as Braus ('05, p. 472) suggests, may not be sharply distinguished from the cell-chain hypothesis which has been rendered untenable or unnecessary by Braus' experiments upon amphibian larvae. Braus admits, however, the possibility of the formation of protoplasmic bridges before the appearance of the neurilemma cells. But, since it has not yet been proved that the protoplasmic bridges are the products of indifferent cells—in other words, that they are not the product of the same neuroblasts which produce the neurofibrillae—the hypothesis remains little more than a speculation, and the phenomena upon which it seems to rely are equally well interpreted by the process theory.

Other investigators, such as Apathy ('97), Joris ('04), Pighini ('04, '05), Besta ('04), London and Pesker ('06), Brock and Gierlich ('06, '07), and Held ('09) have presented some divergent opinions, but no wholly distinct point of view. The peculiar views of Apathy possibly deserve special recognition since they have aroused so great an interest. According to Apathy ('97) the embryonic ganglion cells acquire their fibrillar structure, not by a process of cell differentiation, but secondarily

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from special cells, which, as actual 'nerve cells'—that is, as neurofibril-forming cells—are intercalated in the path of the nerve fibers and which push their differentiated product into the interior of the muscle cell or gland cell as well as into the ganglion cell. This doctrine, which conceives of the ganglion cell and the nerve cell as entirely distinct kinds of cells has been also supported by Bethe ('00–'07). According to Bethe the neurilemma cells are the 'nerve cells' in the Apathy sense of the word. That is to say, they are the cells which have formed the neurofibrils and persist as sheath cells.

Held attempts ('09) to reconcile the divergent views of nerve histogenesis, finding something of truth in them all. In common with Hensen he emphasizes the importance of protoplasmic paths which furnish material for the growing nerve; agrees with the Hertwig brothers that these may be secondarily formed by indifferent cells, and supports the Kupffer-Bidder theory in holding that the neurofibrils are the product of the neuroblast through a process of centrifugal growth. While his observations seem to support the process theory in most details, he denies the doctrine of free outgrowth of nerve fibers.

None of these hypotheses of nerve histogenesis has been abandoned entirely by partisan supporters. With the introduction of special nerve methods the confusion has seemed to increase rather than to diminish, so that there is not a single result of the most recent investigation which is not directly opposed by another. The chief problem raised by Apathy as to the genesis of the neurofibrils, has not yet been solved; and the more important question of how muscle and nerve become connected seems as far from solution as ever. Relief from conflict of opinion has not followed recourse to experimental morphological methods as is shown by the divergence in the views regarding neurogenesis held by Harrison ('03, '04) and Braus ('05). While the former supports the process theory, the latter thinks that his results confirm the Hensen or Hertwig hypothesis of predetermined paths for the growing nerves.

Upon the answer to the question, whether or not nerve and muscle are primarily connected, depends, in large measure, not

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only the answer to the problem of the morphology of the eye muscles and their nerves but also general conclusions regarding the phylogenesis of the vertebrate head. For it may readily be seen that if nerves are ab initio connected with their terminal-organs, all the modifications of the latter would naturally be accompanied by associated changes of the former. If, for example, a post-otic nerve innervates a pre-otic muscle, upon the assumption of an immutable connection of nerve and muscle, the inference that the muscle had migrated from behind the ear into its present position and carried its nerve with it, might appear the most reasonable interpretation of such a peculiar relationship. But if, on the other hand, a nerve is not invariably associated with a given muscle throughout its phylogenetic history, but may grow into muscular territory primitively foreign to it, such an assumption would greatly modify our views of nerve and muscle phylogenesis and possibly our views of the history of the vertebrate head.

The histogenetic problem of neuro-muscular relations therefore appears fundamental to any problem, such as that of the morphology of the vertebrate head, involving nerve and muscle in complex and obviously modified relations. Upon the answer to this problem depends, for example, the answer to the problem of the present singular muscular relations, of the trochlear and abducens nerves. While it is an unquestioned fact that nerve and muscle tenaciously retain connections once acquired, and while this conservatism of relation may be taken as a basic assumption in morphology, the possibility still remains that under changed conditions new neuro-muscular relations may be acquired. If Gegenbaur and Fürbringer be correct, such changes are as incredible as, for example, the inheritance of mutilations are believed to be. But, on the other hand, to all of those who have come to accept the process theory of nerve development and who therefore assume the secondary connection of nerve and muscle, the invasion of new territory and its piratical seizure by exotic nerves appears a possibility. A discussion of the present problem, therefore, does not lead the morphologist far afield. The history of the head must be written primarily in terms of nerve histogenesis.

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The attempt has been made recently by Held ('06, '09) and Paton ('07) to combine the two views of nerve histogenesis, claiming a primary connection of neural tube and myotomes by means of protoplasmic bridges or plasmodesmata, along which, as paths, later the true nerves—neurofibrillae—by centrifugal (Held) or centripetal (Paton) growth—effect the definitive nervous connection with the muscle. True nervous connection with muscle is thus secondary, but the connection takes place along predestined paths—the plasmodesmata.

Whether the plasmodesmatous connections are secondary or primary remains undetermined by Paton. Held (p. 277) holds with the Hertwig brothers ('78) that they are secondary and he states that Hensen's hypothesis that all nerves have arisen through the incomplete separation of the origin and end cells cannot be correct. Held, however, does not appear to have established the truth of this assertion on the basis of a detailed study of their genesis in the vertebrate embryo. The theoretical importance of the manner of establishment of these 'primary' protoplasmic connections of neural tube and their genetic relations to the cells which form the neuro-fibrillae is so great that it appears worth while to consider this portion of the histogenetic problem with thoroughness and in great detail. The functional importance of the primary protoplasmic connections has been established by the valuable experiments of Paton ('07), who demonstrated that in selachian embryos, in stages before the appearance of neuro-fibrillae, the embryo responds by muscular movements to external stimulus. If such reactions be effected through the medium of the central nervous system, then it is certain that the efferent paths of the impulses must be the "undifferentiated protoplasmic bridges" described by Paton and identified by him as the 'plasmodesms' of Held ('06), To some this evidence might seem sufficient to prove their 'nervous' character, but not so to a disciple of von Apathy, to whom there is "no nerve without neuro-fibrillae." With regard to these protoplasmic bridges, Paton has the following to say (p. 555):

In the region of the ventral roots in a 5 mm. embryo of Pristiurus there is a marked bulging forward of the protoplasm and in many sections a 'bridge' about 4 to 5 μ in width similar to those shown by

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Kerr ('04) to exist in Lepidosiren may be seen spanning the distance between the edge of the medullary substance and the inner border of the myotome. The structure of the protoplasm of which these strands are composed seems similar in all respects to that forming the general matrix and does not at any point, except at the places to be described later on, present evidence of a fibrillar structure. Less frequently strands of protoplasm are seen in other localities, as for example at the point where later in the development of the embryo processes of giant ganglion cells (Beard) emerge from the cord, or where the matrix surrounding the cells of the ganglionic masses is in contact with the periphery. Any attempt to determine the moment when these bridges appear and the manner in which they are formed necessitates the consideration of questions of fundamental importance.

Are these structures the product of a single cell or do several elements contribute protoplasm to span the interval between two given points as widely separated as the periphery and cord? Hensen's idea that these bridges are originally thrown across from one cell to another and then as the embryo grows these threads are pulled out to many times their original length, is an exceedingly ingenious and suggestive hypothesis but has not yet been proved. There cannot be any ground however for doubting the existence of these structures. The debatable point is merely in regard to the manner in which they are formed.

Further on he says:

Neal ('03) in an interesting paper on the development of the ventral nerves in Selachians, says that he has been unable in any of his sections to show the existence of a protoplasmic connection 'even of the most attenuated kind between the somite and the neural tube before the first neuraxon makes its exit from the neural tube.' At first it was difficult for me to reconcile this statement with the results of my own observations as well as those of other investigators who have repeatedly observed these bridges in Selachans. At the time when Neal's investigations were conducted there was no method of staining which was capable of differentiating the component parts of the neuraxon, and it is not at all improbable that the structure which he had reason to believe was the growing end of a neuroblast was only the undifferentiated protoplasmic band or bridge. In the second place the method of fixation undoubtedly has something to do with the failure to detect the existence of these structures which are much more easily demonstrable in sections fixed in corrosive—acetic or neutral formol than they are in solutions containing picric acid. For the reasons mentioned the structures represented by Neal as neuraxons cannot be accepted as such without further proof.

Paton goes on further to say (p. 556) that:

Probably the long processes depicted by this investigator as being projected from medullary cells are in reality made up of two com-

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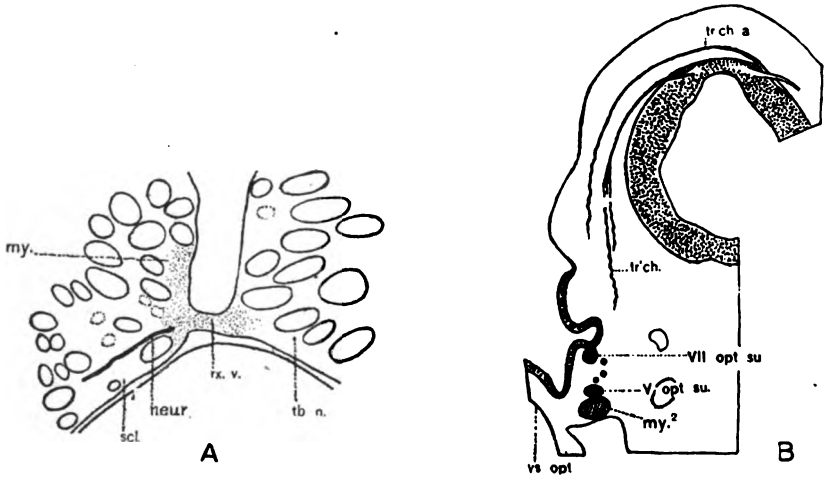
ponents: a short process and the long undifferentiated protoplasmic strand or bridge with which it is apparently fused so as to give, in specimens stained by certain methods the appearance of a single long process. In plate 23, figure 1, one of the bridges is represented, the proximal side of which has fused with the matrix of the cord while the distal is united with that of the myotome. (See text-figure A.)

A similar condition is also depicted in figure 2. At later stages one may find connections present between the cord and group of cells, which eventually form the spinal ganglia, and between the latter and



Text fig. A Taken from Paton's figure 2, plate 23; *my.*, myotome; *neur.*, neuraxon (neurofibril, Paton); *rx.v.*, anlage of somatic motor nerve (plasmodesma, Paton); *scl.*, sclerotome (myotome, Paton); *tb.n.*, neural tube. Paton's figure 1, plate 23, is in all essentials like this, but does not show the neuraxon process (neurofibril) stained.

Text fig. B Taken from Dohrn, 1907, figure 7, plate 21; *my.*,² VanWijhe's second myotome (*m.obl.sup.*); *tr'ch.a.*, peripheral chiasma of the trochlearis; *tr'ch.*, trochlearis anlage; *vs.opt.*, optic vesicle; *V.opt.su.*, ramus ophthalmicus superficialis trigemini; *VII.opt.su.*, ramus ophthalmicus superficialis facialis.

the periphery. Further there is abundant opportunity to study these plasmodesmata (Held) in the region of the cranial nerves, where undifferentiated links of protoplasm frequently unite the existing ganglionic masses either with the central nervous system or with the periphery. In the case of the oclomotorius and trochlearis the existence of these bridges is very problematic.

The present writer ('03) made the attempt to discover whether the protoplasmic bridges of Paton were primary or secondary

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connections of neural tube and myotome and he reached the same conclusion as did Dohrn ('88), namely, that they are secondary in origin and that they arise by the extrusion of processes of medullary cells which Neal regards as neuroblasts. Froriep ('04) stated with equal positiveness that the protoplasmic bridges are connected with intramedullary cells. Against the assertions of these three observers we have the statement of Paton that "probably the long processes depicted by this investigator as being projected from medullary cells are in reality made up of two components: a short process and the long undifferentiated protoplasmic strand or bridge with which it is apparently fused so as to give, in specimens stained by certain methods, the appearance of a single long process."

This assertion taken in connection with Paton's criticism (quoted above) of my results as based upon inadequate methods of preservation and staining suggests the possibility that Paton himself has been unable to reach positive conclusions regarding the histogenesis of the 'protoplasmic bridges' and the relations of their cellular components because of too implicit reliance upon a method primarily suited to demonstrate the neuro-fibrillae but quite unsatisfactory for general cytological purposes. However adequate—or inadequate—the Bielchowsky-Paton method for demonstrating the histogenesis of the neuro-fibrillae, it appears quite unsuited for demonstrating the cellular boundaries and relations. For this purpose, the vom Rath method as used by Neal ('03) is superior. The difference between the cytological results obtained by the Paton method and those obtained by the vom Rath method are strikingly shown by a comparison of Paton's figure 2, plate 23, and figure 11 of the present paper, which represent almost exactly identical stages in the histogenesis of somatic motor nerves. The most striking difference consists in the absence of cell boundaries in the former and in their clear definition in the latter. (See fig. A, p. 25.)

But Paton's failure to determine the histogenesis of the 'protoplasmic bridges' is not wholly due to his failure to use a method of fixing and staining which demonstrates cell boundaries and relations, but there is evidence also that he did not make a

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careful study of the earlier stages in the differentiation of the somite and of the 'protoplasmic bridges.' A study of those earlier stages when protoplasmic connections are formed might have convinced him that Dohrn, Froriep and Neal have stated the facts correctly. That Paton had neglected the study of the genesis of these bridges is evident from his failure to recognize the sclerotome in his sections. For had he been thoroughly familiar with the earlier stages, when the 'protoplasmic bridges' first appear, he would have seen the formation of the sclerotome associated with the development of the bridges and consequently would not have been led to the inference that the primitive fibrils of somatic motor nerves make their first appearance within the myotome. Held ('09, p. 253) has already called attention to this.

The origin of the neurofibrillae and their relation to the protoplasmic processes which form the protoplasmic bridges will be discussed in a later section of this paper in connection with the problem of the genesis of these plasmodesms. This is the essential point of difference between the results of Paton and the writer. I have regarded the medullary processes which form the 'protoplasmic paths' as neuraxon processes, since the neurofibrils are differentiated within them. These processes were therefore spoken of as neuraxons and the statement was made that "before the first neuraxon makes its exit from the neural tube, sections show no protoplasmic connection, even of the most attenuated kind, between the neural tube and the somite." Paton, holding the Apathy view of the independent and exogenous origin of the neurofibrils recognizes no neuraxon—not even an undifferentiated neuraxon—in the absence of neurofibrils. And yet, as Paton has demonstrated in the case of the Rohon-Beard cells, the neurofibrils become secondarily differentiated within the neuroblast and its process, which consisted primarily of undifferentiated protoplasm. The proof that the protoplasmic bridges are formed by neuraxon processes will be stated later in this paper.

If Paton ('07, p. 556) be correct in thinking that the trochlear and the oculomotorius acquire their nervous connections with their muscles without the participation of plasmodesmatous

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bridges, a conclusion reached by Neal ('98), Dohrn ('07) and Gast ('09), there appears no good reason why he should not accept the conclusion that spinal somatic motor nerves become differentiated and connected with their myotomes in the same manner. If a nerve like the trochlear, which traverses a great distance in reaching its peripheral organ, can do so without the aid of a plasmodesmatous bridge, there would seem very little ground for assuming a different mode of histogenesis for spinal somatic motor nerves. That, as a matter of fact, their genesis is essentially alike is supported by the evidence presented in this paper,

Held ('06, '09) like Paton ('07) emphasizes the importance of the plasmodesmatous connections of neural tube and myotome, and concludes, in agreement with O. and R. Hertwig ('78), that these plasmodesmatous bridges are secondarily formed as cell outgrowths. Not only cells of the myotome and spinal cord but also those of the chorda are supposed by Held to participate in their formation. Held ('09, pp. 91–92) refers to the network between chorda, tube and myotome as 'Scilly's Fasernetz' and characterizes it as usually a cell- or nuclear-free tissue, since it consists exclusively of the basal cell processes of the germ layers united together. Secondarily, mesenchymatous cells wander into this network.

He further states (p. 281) that at the time of the appearance of the first motor nerves, which have grown from the neural tube, there is everywhere present an abundance of fine connections. The process of transformation of this—a pre-nervous plasma path—into nerves depends upon the specific power of His' neuroblasts.

With regard to their primary origin, he says (p. 277) that Hensen's hypothesis that all nerves have arisen by the incomplete separation of the origin- and end-cells cannot be correct, since it cannot be thoroughly applied to the details of the development of definite organs in their reciprocal relations. The motor spinal nerve of a frog-larva, for example, can be developed from no mitotically-formed primitive nerve. On the contrary, Held, in agreement with the Hertwigs, regards the plas-

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matic connections which form the nerve paths as secondary in origin. He has, however, failed to make a detailed study of the genesis of those plasmodesmata which, according to his view, are later transformed into the somatic motor nerve anlagen. Furthermore, one searches in vain through Held's admirable monograph for a convincing proof of the assertion (p. 274) that "the growth of the nerve substance is correlated with a resorption of the plasmatic path so that the latter passes over into the former and is utilized in its formation." Similarly unproven is the dogmatic assertion (p. 280) that the 'plasmatische Ausflüsse' of Dohrn ('88) are really not such. Dohrn's characterization of the first protoplasmic connections of tube and myotome as 'plasmatische Ausflüsse' seems admirable. That they quickly lose this undifferentiated protoplasmic character may readily be granted, so that Held's assertion is correct except for the very first stages in the appearance of the protoplasmic bridges.

A number of important questions are involved in the issue raised by Held and Paton: (1) Are protoplasmic connections between myotome and tube primary or secondary? (2) What cells participate in their formation? (3) Have these protoplasmic paths a genetic relation to the neurofibrils? That is, do the same cells which form the plasmodesms also differentiate the neurofibrillae? The writer ('03) concluded that the protoplasmic connections are secondary; that they are formed exclusively by processes of medullary neuroblasts; that within them the neurofibrils are differentiated. Paton ('07) was not able to determine whether they are primary or secondary; suggests (p. 560) that mesenchymatous cells may participate in their production; and concludes that the neurofibrils have no genetic relation with the protoplasm of the bridges, but arise independently within the myotome and grow centripetally into the tube along the bridges. On the other hand Held ('06, '09) regards the plasmodesms as secondary in origin; but holds that they are formed by the fusion of cells of chorda, tube and myotome; maintains that they have no genetic relations to the neurofibrils which grow into them secondarily from medullary neuroblasts, for which the paths provide a protoplasmic covering. The great theoretical importance

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of these problems warrants a reinvestigation of those stages in vertebrate embryos which may contribute to their elucidation. Taking up these problems in order we may first ask whether or not protoplasmic connections between myotome and tube are primary or secondary.

1. Are muscle and nerve connected with each other ab initio? The Hensen view of the primary connection of nerve and muscle is not supported by the evidence presented by Squalus embryos as shown in the drawings represented in figures 1, 2 and 3, which demonstrate the relations of tube and somite in stages previous to the appearance of the anlagen of somatic motor nerves. Figure 1 may seem the most significant of the three since it is taken from a series in which no somatic motor nerve has made its appearance anywhere in the embryo. The section is typical of the trunk region of embryos of this stage and the finer histological features are in all essential respects like those presented by standard methods of preservation and staining. That the space between tube and somite is normal and not an artifact is evinced by the fact that it appears in the living embryo. In sections this region appears to be filled by a vacuolated non-staining or slightly staining plasma. The most significant fact presented in the section is the absence of protoplasmic bridges between tube and somite. Before the first anlagen of the motor roots make their appearance in later stages, it is impossible to find protoplasmic connections between the two organs. The kind of fixation or the stain used makes no difference in the phenomena, provided the space is not obliterated through shrinkage. Reagents, which like formalin cause considerable plasmolysis and vacuolization, and the use of which is likely to be followed by considerable shrinkage, may exaggerate the vacuoles and cause their confluence so that the granular material, which in Flemming or vom Rath preparations is quite evenly distributed, as shown in the drawing, becomes aggregated in denser strands and may simulate protoplasmic strands extending between tube and myotome. However it does not stain like protoplasm, even when aggregated in the manner suggested,

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and for this reason has been universally ignored in all drawings. Paton ('07), for example, does not indicate its presence in the sections figured by him (figs. 1 and 2, pl. 23) although it is undoubtedly present in those stages. It may not be confused with the protoplasmic paths emphasized by him and Held ('06, '09).

The plasmodesms of Held ('09) appear to be formed by the union of the plasmoid material of the intercellular spaces with the amoeboid protrusions of the basal cells of the germ layers. At the stage represented in figure 1, protoplasmic processes are lacking in the case of the neural tube, the outside boundary of which consists of an imperforate basal membrane. The chorda is likewise without protoplasmic outgrowths. The median surface of the somite, however, shows a few short and inconspicuous amoeboid extensions. However, between the homogeneous, slightly stained protoplasmic outflows of the somitic cells and the unstained, granular material of the vacuolated plasmoid material between the germ layers, there is distinct contrast, although the two appear to connect with each other. In the drawings the plasmoid substance is greatly exaggerated in order to show it at all. As has been stated, it has been generally overlooked in most embryological studies.

Even when the films of plasmoid material coalesce as the result of reagents, they require intense stains and special illumination to make them visible. They form a most attenuated material for the production of nerves. It would seem most unlikely that growing nerves would trust themselves to such flimsy paths as guides to their destination. That students of nerve histogenesis should seriously consider such all-but-invisible films of non-protoplasmic material as the substance or path of a growing nerve suggests that followers of the Hensen hypothesis are in desperate need of a material basis for their assumptions. In no true sense do the plasmoid films constitute a primary protoplasmic connection between tube and somite. The actual protoplasmic connections are effected secondarily as the following evidence shows.

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3. What cells contribute to the genesis of protoplasmic connections between tube and somite? What cells form the first anlagen of spinal somatic motor nerves?

In stages slightly later than those just described, protoplasmic processes are extended into the intercellular space between tube and somite by cells of neural tube and somite. In the regions in which nerve anlagen later make their appearance protoplasmic movement makes its first appearance sometimes from somitic cells and sometimes from cells of the neural tube (figs. 2, 3 and 4). In either case the ends of the projections appear connected with plasmoid films. But the first real protoplasmic connections between tube and somite are formed by the outflows of medullary cells (fig. 4).

In subsequent stages the reciprocal movement of medullary protoplasm and mesenchymatous cells (sclerotome) results in the close approximation of the two sets of protrusions and in exceptional cases, such as are shown in figures 8 and 9, the two appear indistinguishable. Such close approximation is rare and, when it occurs, appears temporary, so that the genetic relations of medullary cells to the protoplasmic bridges between tube and somite seem indisputable.

Those medullary cells, which by their protoplasmic outflow, effect the first protoplasmic connections between tube and somite usually stain more deeply than the adjacent cells, a fact to which attention was first called by His ('79). The same peculiarity distinguishes the Rohon-Beard cells during analogous stages in histogenesis; that is to say, in the stages of neuraxon production. These 'neuroblasts' of the somatic motor nerves are bipolar in shape (figs. 4–11), and within them may be detected, in suitable preparations, a neuro-reticulum with intensely stained fibrils. The reticulum does not appear to be limited to one pole of the neuroblast cell but extends around the nucleus. To its presence may be attributed the deeply staining properties of the neuroblasts. The fact that neurofibrillae make their appearance in the extended processes of these cells sufficiently evinces their neuroblastic character.

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Kerr ('02) was led to doubt the hypothesis of the secondary connection of somite and tube on the ground that in the earliest stages, when somatic motor nerves are visible in Lepidosiren the tube and the somite are in immediate contact with each other: "Lepidosiren thus affords a definite anatomical basis for the view that the nervous bridge between nerve center and end-organ exists from the beginning, and that the growth of the nerve is a drawing out of this bridge as the end-organ is pushed away by the development of the underlying mesenchyma." On the basis of such evidence Kerr concluded that the Hensen hypothesis is 'almost demonstrated.'

This inference seems to be a non-sequitur from the evidence presented, since Kerr has traced the anlagen of the somatic motor nerves only to those stages when the protoplasmic connections are already established. Neumayer ('06, page 54) has already called attention to the fact that the stages described by Kerr correspond to advanced stages of histogenesis. If tube and somite in Lepidosiren be normally in contact in early embryonic stages, it would seem to be a form little suited to the requirements of an investigation of the primitive connections of nerve and muscle. Squalus embryos, in which a space is normally present, would seem much better objects of research. The normal distance between tube and myotome in Squalus is so small, however, that the theoretical objection that it would be difficult to explain the growth toward the muscle as a tropism is not likely to be suggested. If the direction of growth of the neuraxon processes of the medullary neuroblasts were determined chemotropically by secretions of the myotome cells there would be little chance for the neuraxons to go astray through a mixing or diffusion of specific secretions. In such a case the theoretical necessity for predetermined paths emphasized so strongly by Held ('09) does not appear very convincing. The difficulty of explaining how the extended processes of Rohon-Beard cells reach their area of distribution by a chemotropic response is much greater, but Held can hardly expect that his speculations (page 274) as to the stimulation of the neuroblast process through predetermined plasmodesmatous paths will be regarded as pref-

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erable. But this theoretical difficulty loses its force when applied to the connections of organs in such close proximity as are neural tube and mytome in the trunk region of vertebrate embryos.

To summarize the evidence that connection between neural tube and muscle segment is formed by protoplasmic movement of medullary cells, we have first the fact that in early stages no protoplasmic connections between tube and somite are found. A plasmoid substance fills the space between tube and myotome. Later, medullary cells in the ventro-lateral wall of the tube develop a neuro-reticulum and manifest deeply staining properties. This change is followed by a protrusion of amoeboid processes into the space between tube and somite. Later such protrusions become wider and more extensive, several adjacent cells adding to the size of the protoplasmic bridge thus formed between tube and myotome. The movement of medullary protoplasm is correlated with a migration of sclerotome cells into the space between tube and somite but the latter elements participate only temporarily, if at all, in the formation of the ectoderm-mesodermic connection.

In this manner are formed the anlagen of somatic motor nerves, which at first appear non-fibrillar and protoplasmic and entirely devoid of cells. These are the protoplasmic bridges of Paton ('07). Later the neuroblastic processes extend ventrad, along the median surface of the myotome and in close contact with it and the sclerotome (figs. 10-11). Medullary nuclei soon begin to wander into the anlage from the tube and the movement becomes so extensive that the form of the tube in cross section is greatly changed (fig. 12). All these stages may readily be seen in cross-sections of a Squalus embryo of Balfour's Stage I, by comparing sections beginning with the cloacal region and passing forward toward the head. Connections in the cloacal region at this stage are still unformed, while the movement of medullary cells has already begun in the more anterior metameres of the trunk.

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4. Have these protoplasmic connections a genetic relation to the neurofibrils?

Paton decides adversely to the view that the protoplasmic bridges are formed by the processes of neuroblasts on the ground that they do not contain fibrillae. He does not deny, however, that "under certain circumstances a nerve cell may throw out a process of very considerable length." But he thinks that "the greatest caution should be observed in assuming that mere length of process, without positive knowledge regarding the nature of the structures contained in it, is in any sense to be considered a criterion as to whether a cellular prolongation is or is not to be called a nerve." To "refer to an undifferentiated tract as a nerve would give rise to endless confusion."

Paton ('07, p. 560) finds that in sections fixed in sublimate-acetic and stained by hematoxylin-eosin, the medullary cells appear 'faintly fibrillar;' but he thinks that this 'primitive fibrillation' has no connection with the development of the neurofibrils.

In his opinion, the conclusions of those who claim a connection between the primitive ventral root fibrils and medullary cells are based upon faulty technique. "No reliable method of staining has yet been employed that is capable of demonstrating the presence of processes in the vicinity of the distal ends of these primitive filaments." According to Paton, the first neurofibrils or 'primitive fibrils' make their appearance within the myotome at a point remote from the protoplasmic bridges, as shown in Paton's figure 2, plate 23, shown in outline in text-figure A of this paper (p. 25).

The primitive neurofibrils are coarse, deeply stained structures appearing primarily in a locality where more than in any other place the ground substance, even after sublimate fixation, seems to be granular in character, while the more delicate and attenuated filaments only become visible at later stages. . . . . The apparent independence of these primitive neurofibrils in the ventral roots from cells is one of their distinguishing characteristics, but in the large cells of Beard a different arrangement exists. There the fibrils appear in the apical process of the cell close to its nucleus (compare figure 2 with figure 12, plate 23).

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Thus Paton not only doubts the neuroblastic origin of the connections between the tube and myotome but also the neuroblastic origin of the neuro-fibrillae. That he has been led into error in his inference of the independent origin of the neurofibrils will be suggested by a comparison of Paton's figure 2 with figure 12 of this paper. Paton is mistaken in his inference, partly because of his failure to trace carefully in earlier stages the genesis of the protoplasmic bridges; partly because he has not used a method suitable to demonstrate cell boundaries, and partly because the neuro-fibrillae in his preparations are incompletely stained, as has already been stated by Held ('09). A comparison of Paton's figure 2 with figure 12 of this paper shows that the 'primitive fibril' which Paton thinks arises within the myotome actually lies between the myotome and the sclerotome. Moreover, its position corresponds with the position of the termination of the cell processes of medullary cells. The two drawings strikingly show the difference in the histological results of the vom Rath and the Bielchowsky-Paton methods. The great advantage of the former appears in the sharp definition of the cell boundaries, of the latter in the clear differentiation of the neurofibrils. The convincing proof given by Held ('09) of the endogenous origin of the neurofibrils within medullary neuroblasts certainly warrants the inference that the neurofibrils are incompletely stained by the Bielchowsky-Paton method. Later in his paper Paton admits the possibility that the neurofibrils are genetically related to the processes of the medullary cells. But he thinks that new technical methods are needed in order to solve the problem thus raised. To determine this, however, needs not so much a new method of neurological technique as a careful study of the successive stages in their differentiation by methods which we now possess, especially a method like the vom Rath which defines clearly the cell boundaries and relations. Paton's procedure admirably supplements such a method.

Held ('06, '09) has made a most thorough and painstaking investigation of the histogenesis of the neurofibrils on the ground that, as stated by Max Schultze, von Kupffer and von Apathy, these are the distinctive structures of the nerve fiber. In agree-

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ment with Apathy, Held is of the opinion that the solution of the problem of the devolopment of nervous tissue depends primarily upon the demonstration of the place and manner of origin of the neurofibrillar substance. He concludes that this important nervous element is differentiated within the neuroblasts of His, which are thus the essential nervous cell centers. These results are in harmony with the experimental results of Harrison, Lewis and Burrows.

Held finds that the first and surest histological characteristic of a cell of neuroblastic tendency lies in the occurrence of a specific network or neuro-reticulum which appears in a circumscribed region of the neuroblast in the vicinity of the nucleus. In the course of its development this network undergoes an extraordinary complication and extension of its substance. The observation of the primary appearance of the neuro-reticulum within the neuroblast had previously been made by Besta ('04).

Contrary to the opinion expressed by His, Held affirms that it is not the outflow of protoplasm into a cell process, but the definitely directed growth of a new and special cell substance which originates the first nerve trunks in the embryo. The process is not that the cell produces a protoplasmic elongation of the cell body in which subsequently and secondarily a fibrillar substance appears. On the contrary there are inner changes within the protoplasm of a neuroblast that lead eventually to the differentiation of a neurofibrillar substance which, while primarily of a minimal extension within the fibrillogenous zone of the neuroblast cell, later in the course of its special growth undergoes a mighty extension in the body after it has produced externally the pear-shaped form of neuroblast first observed by His. This fibrillar structure of the neuroblasts is 'neurofibrillar' in the von Apathy sense of the word.

Held's conclusions do not agree with those of von Apathy ('98) who holds that the ganglion cells produce no neurofibrils but are secondarily penetrated by them. According to Apathy, the neurofibrils are produced by other and special cells—the 'nerve cells'—which are not to be confounded or identified with 'ganglion cells.' The 'nerve cells' produce, ac-

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cording to von Apathy, the conducting or neurofibrillar substance just as muscle cells produce muscle fibers. From these 'nerve cells' the conducting substance grows on the one hand toward the center in the 'ganglion cell' and on the other hand toward the periphery into the sensory cell or muscle cell and so forth. The nuclei of the nerve cells lie in the course of the nerve fibers themselves and form in vertebrates the nuclei of the neurilemma sheath. The protoplasmic body of the nerve cell is, in general, spindle-shaped so that it may be called the nerve spindle. Its membranous boundary is the neurilemma.

For every motor nerve fiber of a vertebrate, on the other hand, according to Held, there may be distinguished a central and peripheral nerve stretch. The external limiting membrane of the neural tube divides the two. The neurofibrillae of the central stretch are formed before the peripheral. They arise through the unilateral growth of the neurofibrillar substance of a unipolar or bipolar neuroblast which proceeds basalwards in the direction of the Rabl's 'chief axis' and soon transcends the outer limits of the neural tube in its growth toward the terminal organ. The central stretch of the nerve varies with the position of the neuroblast cell. In its extent through the marginal zone the nerve fiber becomes secondarily surrounded and enclosed by glia cells.

Held distinguishes three chief stages in the development of the peripheral stretch of the nerves:

1. That of the outgrowing nerve itself, which has not yet reached its terminal organ with its specific substance, but nevertheless is connected with its terminal organ by means of a simple undifferentiated plasmodesmatous strand. Theoretically this stage is the most important. The His doctrine, according to which the amoeboid neuroblast processes extend through open spaces in the tissues, cannot be correct, since in the Anamnia the growing point of the motor nerve is connected with portions of the epithelium, that is by plasmodesmatous connections, and in the Amniota on the other hand with parts of the mesenchyma.

2. In the second stage the nerve has reached its muscle anlage, which it not only touches superficially, but cells of which

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it penetrates with its neurofibrils. At this stage the motor nerve anlage in Anamnia is non-cellular while in Amniota it is cellular. The cause of this difference is as follows: In case the nerve anlage makes its appearance while the germ layers and the anlagen of the organs are still epithelial as in the Anamnia, the peripheral neurofibrillar tract lies in nuclear-free and net-like plasmodesms, which connect the related epithelial surfaces with each other. If, on the other hand, a connective tissue is already developed, then such nerve fibers extend through a variable number of cell-bodies. In the first case the nerve appears primarily without nuclei, while in the second it appears as a nucleated structure. The difference is due to a difference in the relative time of differentiation of the neuroblasts.

3. The third stage is a transition to the condition in the adult nerve with its cellular neurilemma sheath, and arises through the emigration of medullary cells into the fibrillar nerve and their differentiation as sheath cells.

Held summarizes his views regarding the histogenesis of motor nerves as follows:

The origin of motor nerves rests upon the peripherally directed growth of the specific cell substance of definite neuroblasts of the neural tube and which proceeds in the direction of the chief cell axis of the neuroblasts, and, for definite but unkown reasons, transcends the outer boundary of the embryonic neural tube. A stage of development precedes the formation and growth of the nervous substance itself, by means of which the neural tube and its motor neuroblasts, through net-like arranged paths of a simpler and not yet neurofibrillar substance, is brought into connection with the peripheral muscle anlage by complicated processes of outgrowth.

Such connection paths, which in Anamnia are simple and epithelial and in the Amniota, on the contrary, are a complicated connective tissue, are in the Hensen's sense of the word 'used' by, and in some sort of an unknown manner fused with, the nervous substance growing from the neuroblasts. The growth of the nerves to the terminal organ does not proceed in the liquid-filled vacuoles of the intercellular spaces as affirmed by His, since the growing points of the nervous substance are connected both laterally and at the outer extremity with the farther-reaching plasmodesms of the surrounding tissues. Later, by means of complicated processes of multiplication and movement of medullary cells, which wander secondarily into the primarily non-nuclear, or nucleated, nerve-path as cell-elements organically connected with it, the motor nerve becomes the multinucleated strand supplied with

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neurilemma cells. The cell-chain hypothesis has entirely looked upon and conceived the beginning of this third stage as the actual beginning of the specific formation of nervous substance. Actually, however, this condition belongs to that period of the development which transforms the embryonic type of nerve into the adult and differentiated structure.

In presenting evidence of the secondary connection of nerve and muscle, and perhaps more convincingly, evidence of the endogenous origin of the neurofibrils and their genetic relation to the medullary neuroblasts, Held supports the essential points of the process theory of nerve development. His conclusions, however, differ from those usually held by supporters of the Kupffer-Bidder theory in regard to the origin of protoplasmic connections of nerve center and end-organ. In this regard Held considers himself an advocate of the Hertwig theory, since he holds that protoplasmic connection of tube and myotome is formed, not by the neuroblasts which form the neurofibrils, but independently as plasmodesms of indeterminate and multicellular origin.

There is nothing in Held's monograph, however, to indicate that he has given as careful attention to the development of these plasmodesms as to the histogenesis of the neurofibrils. The evidence presented by the writer ('03 and in the present paper) supports the view of His, von Lenhossek, Cajal that the same cells which form the neurofibrils also form the protoplasmic connections between tube and myotome. In other words, the neuroblasts themselves form the protoplasmic connections of tube and myotome. As shown in plates 1 and 2, the processes of medullary neuroblasts extend along the median surface of the somite between myotome and sclerotome and within these processes (which may be traced to their connections with medullary cells as stated by Froriep, '04) neurofibrils make their first appearance as is clearly shown in preparations made by suitable methods of staining. In the light of Held's results, it seems probable that a neuro-reticulum is present within the neuroblast cell, but no method sharply differentiates it in Selachians in early stages of histogenesis. Sometimes in Bielchowsky-Paton preparations a fibrillar network appears in certain medullary cells in stages before protoplasmic connection with the myotome has been formed. That this is neu-

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rofibrillar has not been demonstrated, however, although the analogy of the histogenesis of the Rohon-Beard cells would favor this opinion.

Although the evidence presented in this paper is not sufficient to demonstrate positively that the neurofibrils of somatic motor nerves arise endogenously within those medullary cells which form the protoplasmic connections of tube and myotome, the conclusion that such is the case appears justified on the following grounds:

1. The evidence goes to show that medullary cells, by a process of outgrowth, form the first protoplasmic connection of tube and myotome.

2. In subsequent stages these processes extend ventrad along the median surface of the somite between myotome and sclerotome.

3. Within these processes which in vomRath preparations may be traced to their connection with medullary cells, the neurofibrillae make their appearance.

4. Since, as shown by Paton ('07) the neurofibrils arise endogenously within the processes of Rohon-Beard cells, and Besta ('04) and Held ('06, '09) have demonstrated a similar histogenesis in somatic motor neuroblasts of Amniota, analogy would seem to support a similar origin in Selachians.

Coghill ('13) has been able to demonstrate that in Amblystoma the neurones of the somatic motor column become well differentiated and typically oriented in the spinal cord before the ventral roots appear at the corresponding level. The earliest demonstrable root fibers arise as collaterals from these neurones, usually from descending processes.

5. *Is the neuraxon of a somatic motor fiber multicellular in origin, or is it the process of a single medullary cell?*

Since the beginning of the twentieth century the Schwann-Balfour 'cell-chain' theory of nerve development has been supported by Rafaelle ('00), Bethe ('00-'07), Oscar Schultze ('04-'07), Brachet ('05-'07), Cohn ('05-'07) and possibly von Apathy ('07). From its inception the cell-chain hypothesis has depended

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for its support largely upon the well established fact of the cellular structure of embryonic nerves. It was this fact that caused Kupffer finally to abandon his process theory. Then also von Apathy's important discoveries of the intercellular relations of the neurofibrils have seemed to some to favor this view of neurogenesis, so that the theory appears to have a new lease of life. Bethe ('03) is of the opinion that he has established the fact of the dependence of the axis cylinder upon the 'nerve cell'—in the Apathy sense—because he finds that in his preparations the mitotic division of a nucleus interrupts the nerve fiber. Held ('09) suggests that this evidence might warrant another inference not complimentary to the quality of Bethe's preparations. Taken as a whole, the arguments in favor of this much discussed hypothesis, which has derived the larger part of its support from preparations unsuited to the requirements of neurological investigation, seem most unconvincing.

Held's ('09, p. 51) discovery of the polyneuroblastic origin of nerve fibers should not be taken as a confirmation of the cell-chain hypothesis, since it does not involve the idea of a cell-chain but asserts the formation of some neuraxons by the fusion of the processes of adjacent neuroblasts.

Bardeen ('03, p. 255) and the writer ('03) have advanced arguments against the claim that the cells of embryonic nerves participate in the formation of the fibers of the nerves. In this connection, Bardeen says that "in an early embryonic nerve of moderate size one finds many hundred fibrils enclosed by a sheath of flattened cells, but with no cells among them. In such nerves one can most easily see that the fibrils are not differentiated parts of cells lying in the nerve."

The phenomena of motor nerve histogenesis in Squalus affords no support to the cell-chain hypothesis, since somatic motor nerves in this animal acquire connection with the myotomes and a fibrillar structure before cells make their appearance within the nerve anlage. The cellular structure emphasized by the advocates of the hypothesis appears only in somewhat advanced stages in histogenesis. Evidence that the cell elements present in the nerve anlagen have a genetic relation to the fibers or neu-

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rofibrils is wholly lacking. Proof that they form the neurilemma has been given by the writer ('03) and by Carpenter ('06).

6. *How does the elongation of the neuraxon take place?*

Does the elongation of a nerve involve simply a migration of protoplasm from the neuroblast cell as the recent experiments of Harrison ('04, '11), Lewis ('06, '07) and Burrows ('11) seem to prove? Or does the neuraxon fiber grow by the progressive differentiation of a primary plasmatic connection between tube and myotome as Sedgwick ('94) and Held ('07) have suggested?

Are we to accept Cajal's evidence of the free termination of the neuraxon fiber in the intercellular spaces of the embryo? Or shall we agree with Held ('09) that "in the growing nerve we have to do with an organically advancing growth, and not with the pushing through of a cell process?"

Although the raising of these questions takes us back to the time of von Baer and the beginnings of embryology, it cannot be said that they have been finally answered. Indeed, the problem of how the elongation of the neuraxon process is effected remains one of the most vexed questions of histogenesis.

Cajal ('07) describes the nerve fibers as advancing and growing through the mesoderm, using the cellular interstices. To him the 'Leitzellen' and their anastomosing expansions are always situated on the sides of the axons which, as the result of the disturbing action of the reagents (pyridine, alcohol), attach themselves to, or partially unite with, the mesodermic framework. To Held ('09) such evidence of nerve terminations ending freely in the intercellular spaces is a result of the rupture of the plasmodesms, with which he affirms the growing tip is normally connected. The growth of the nerve substance he states (p. 274) is correlated with a resorption of a plasmatic path so that the latter passes over into the former and is utilized in its formation.

Harrison ('01) states that the sensory nerves of Salmo salar possess fine lateral branches "which might easily be confused

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with coagulation threads, which are everywhere present," but, unlike Held, finds no genetic relations between such coagulation threads and the elongating neuraxon process. Later ('07) Harrison writes that "it is by no means certain that the plasmodesms are not artifacts—products of coagulation," and von Lenhossek ('06) offers the same criticism.

Such criticisms suggest to Held ('09) that Cajal and Harrison have not seen the true plasmodesms, which are not only very easily ruptured but appear everywhere different from coagulation threads. They may be covered with coagulation bodies, or not; that varies with individual preparations. If, however, one has ever seen these fine plasmodesmata branch out in characteristic fashion from subdividing and branching cell processes, it is impossible longer to hold the view that these fine and definitely branching threads are coagulation products or artifacts.

Held emphasizes the delicacy of the plasmodesmata and the ease with which in fixation or imbedding and sectioning they may be ruptured and lost. While this is unquestionably true, it is also a fact that the plasmodesms become more conspicuous in preparations in which there has been excessive plasmolysis and vacuolation, as in many preparations made for special neurological purposes. On the other hand, the more faithful the cytological fixation, the less conspicuous becomes the coagulable substance found in the intercellular spaces where the neuraxon processes of medullary neuroblasts and those of Rohon-Beard cells grow towards their end-organs.

While Held (p. 297) admits that Harrison's experiments prove that processes may grow out from neuroblasts in suitable fluids, that nerve elongation may occur exclusively by protoplasmic movement and therefore does not necessarily involve the participation and differentiation of plasmodesms, nevertheless he maintains that a normal nervous system oriented to the terminal-organ is formed only with the participation of plasma connections already present. If, however, it may be assumed that the experiments of Harrison ('04–'11), Lewis ('06, '07); and Burrows ('11) throw any light upon normal processes of histogenesis—a conclusion which Held does not seem willing to admit

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—they tend to show that however important the plasmodesms may be as guides for the growing nerve, their share in its production is negligible. They prove as convincingly as experimental data possibly can the logical fallacy of Held's inference, that because the growing tip of the neuraxon is connected with branched plasmodesmatous processes that therefore these processes have a genetic relation to the neuraxon. The significant fact in this connection is that Harrison's preparations show these same processes at the termination of the neuraxons growing freely in salt solutions! The genetic relations are here precisely the opposite to those inferred—or assumed—by Held in the normal growth of the neuraxon. Even if it be admitted that Held's assertion is correct that the growing and more or less branched point of growth of the nervous substance at its extremity possesses, in advance of its momentarily attained length, a projecting extension which connects (as an undifferentiated plasmatic mass between the termination of the growing nerve and the end-organ), the neuroblast with the terminal-organ, his conclusion, already quoted, that the plasmodesm is utilized in the formation of the nerve is a logical non-sequitur. Nowhere in his excellent monograph does Held give adequate evidence to prove this assertion, and the experimental evidence seems to make the assumption unnecessary. Furthermore, the assertion that the growing termination of the neuraxon is connected by a strand of undifferentiated protoplasm with the end-organ has not been demonstrated.

As further evidence in favor of the view that neuraxons and neurofibrils are differentiated within plasmodesmatous or protoplasmic strands, and consequently in conflict with the idea that they grow 'naked' into the vacuolar spaces of the embryo, Held emphasizes the fact that from their first appearance the neurofibrils appear surrounded by a layer of granular protoplasm, a relation better seen in cross-sections than in longitudinal ones. On the other hand, von Lenhossek ('06) states, on the basis of observations on the histogenesis of spinal nerves in the chick, that "first and foremost is it untrue that the young fibers are embedded in protoplasm" but that on the contrary, "the fibers

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lie definitely free, and in the spaces between them there is not the slightest amount of protoplasm to be seen. Held denies the accuracy of this description as based upon unsatisfactory methods of preservation and staining. Cajal ('06, '07) in Held's opinion has been led into error for the same reason. On the other hand, Kölliker ('05) finds the fibers of the embryonic trochlearis nerve in a calf surrounded by sheaths of an intermediate substance. Gurwitsch ('00) mentions a lamellar network which grows into the bundle of 'naked' fibers from the surrounding mesenchyma sheath and divides up the nerve bundle, while according to Kappers ('04) the nerve bundle is coarsely split or divided by fine processes of the neurilemma cells.

In his search for evidence to support the hypothesis of the plasmodesmatous origin of nerve fibers, it seems not to have occurred to Held that the protoplasmic envelope of an embryonic nerve fiber may be produced by the same neuroblast that formed the fiber. The simple fact of a protoplasmic sheath around the neurofibrillae no more proves the existence of nerve 'paths' than it does the hypothesis of neuroblastic outflow. The evidence is in harmony with either supposition. In Squalus, embryonic nerve fibers are 'naked' in the sense that primarily they have no cellular sheaths. But it is also a fact that they have granular, protoplasmic sheaths, visible, not only in sections, but in cover glass preparations of the living nerve fiber. The substance of the sheath stains lightly under the same treatment which stains the fiber intensely. For this reason the protoplasmic envelope is easily—and has been generally—overlooked. The thickness appears to vary in proportion to the length of the neuraxon process. In nerve anlagen, like the trochlearis, for example, in which the fibers are especially long and slender, the protoplasmic sheaths of the fibers are proportionally thin. In spinal somatic motor nerves the sheaths are relatively thick, becoming thinner as the nerve fibers increase in length. The ingrowth of processes of neurilemma cells described by Gurwitsch ('00) and Kappers ('04) occurs in later stages and adds to the interfibrillar protoplasmic substance.

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The intraplasmatic position of the nerve fiber or neurofibrillar bundle, therefore, instead of proving the doctrine of primary plasmatic nerve 'paths,' is equally in harmony with the process theory of nerve development. An examination of Squalus embryos shows that, sooner or later, within the plasmatic neuroblast process which effects the first connection between tube and somite, the neurofibrillar bundle is differentiated as an axial fiber surrounded by the undifferentiated protoplasm of the neuroblast process. The advancing end of the nerve consists of undifferentiated protoplasm and is amoeboid in appearance. The phenomena in sections of preserved embryos are essentially identical with those in vitro of the living nerve fiber. The elongation of the neuraxon, therefore, instead of involving the use and incorporation of primary plasmodesmatous paths into the growing nerve, on the contrary is effected by a movement of the protoplasm of a neuroblast cell and the endogenous differentiation of the neurofibrils. With especial clearness are the phenomena strikingly shown in the giant cells of Rohon-Beard.

a. The histogenesis of the cells of Rohon-Beard. The conclusions based upon the study of the histogenesis of spinal somatic motor nerves are greatly strengthened and confirmed by the phenomena presented by the development of the cells of Rohon-Beard. These phenomena are presented in figures 13 to 22. The close propinquity of the nerve center (neural tube) and the terminal-organ (myotome) in the case of the spinal somatic motor nerve makes it very difficult to find wholly convincing evidence of the extension of the neuraxon process, and of the secondary nature of the connection between the two organs.

In the case of the Rohon-Beard cells, however, the neuraxon process, in reaching its peripheral termination, grows into and through spaces where mesenchymatous cells are entirely absent. As shown in figures 13 to 16, the neuraxon process appears primarily as an amoeboid extension of a large, deeply stained cell, lying in the dorsal wall of the neural tube. As the neuraxon process becomes further extended, its peripheral termination shows many pseudopodia-like extensions. In some cases

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(e.g., fig. 21), as the neuraxon process reaches the apex of the myotome, some of the pseudopodial processes extend median and some lateral to the myotome. It appears to be undetermined whether, in its further extension, the neuraxon may grow between the myotome and the neural tube or between the myotome and the ectoderm. The significant fact presented by such a section and by all the sections which show the cells of Rohon-Beard with their greatly elongated processes, is that there is not the slightest suggestion of a direct primary connection between the cell and its later connection with the ectoderm in the extra-embryonic blastoderm.

Such relations as are shown in figure 20, afford still further evidence of the genetic relations of ganglion cell and neuraxon. The section shows a Rohon-Beard cell lying at the apex of a sensory ganglion, and which has reached its present position by migration from the dorsal wall of the neural tube. The continuity of the cell body and of the neuraxon and evidence of their genetic relation to each other is more clearly shown than in the case of sections where the Rohon-Beard cell lies within the wall of the neural tube. The objection to the inference that somatic neuraxons are formed as elongated processes of medullary neuroblasts, on the ground that it is impossible to trace the protoplasm of the neuroblast through the wall of the neural tube into the growing nerve anlage is met by the evidence presented in this figure.

Doubt remains only as to the inference that the process is formed by a migration of protoplasm from the neuroblast into the neuraxon. Why not infer that the neuraxon is formed from intercellular bridges in situ? In answer to this question, it is sufficient to state that in the earlier stages when the neuraxons of the Rohon-Beard cells first appear, there are no protoplasmic bridges extending in the direction taken later by the growing neuraxons, but simply a non-staining plasma. Furthermore, it is as logical to conclude that the body of the Rohon-Beard cell shown in figure 20 was differentiated in situ as that its neuraxon was formed in situ. On the contrary, if there be good reason for inferring that the Rohon-Beard cell has reached its present

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position as the result of protoplasmic migration from the neural tube, there is equally good reason for the conclusion that its neuraxon has been formed by the same method.

7. What is the source of the cells of somatic motor cells?

The cellular structure of embryonic somatic motor nerves has been emphasized by many embryologists since Schwann ('39) advanced the cell-chain hypothesis of neurogenesis and since its subsequent revival by Balfour ('77). The question of the source of these cells has never been fully determined. Are they medullary or mesenchymatous in origin?

Balfour ('75) was the first to infer the migration of medullary cells into somatic motor nerve anlagen and this conclusion has been confirmed by many investigators including Dohrn ('88), Beard ('88), Herrick ('93), von Kupffer ('94, '95), Hoffmann ('97), Harrison ('01), Bardeen ('03), Neal ('03), Schultze ('04–'07), Held ('06, '09), Carpenter ('06), Carpenter and Main ('07) and Kuntz ('10–'12). His ('89) and von Kölliker ('92), on the other hand, have denied the derivation of these cells from the neural tube. The former concluded that the cells which appear to be in the process of migration from the tube, are later enclosed by the 'Randschleier' which prevents their escape. If it were otherwise, he thinks, the process would lead to the formation of motor ganglia. To His it appeared quite inconceivable that connective tissue elements could come from the nervous system. The mesenchymatous origin of the cells of somatic motor anlagen has also been assumed by Vignal ('83), von Lenhossek ('97), Kolster ('99), Gurwitsch ('00) and Bardeen ('03). Von Kölliker ('05) came finally to accept the probability of the medullary origin of the neurilemma. According to Marcus ('09), the cells of somatic motor nerve anlagen come from the neural crest.

The fact that sclerotome cells are in close proximity to the somatic motor anlagen has led some students to infer that the cells present in later stages within the nerve have had a mesenchymatous derivation. In fact, the mesodermal origin of all connective tissue cells has seemed so well attested that many

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have taken for granted the mesenchymatous nature of all cells associated with motor nerve anlagen. Kerr ('04) seems to have made this assumption for the cells associated with the somatic motor anlagen of Lepidosiren. He says (p. 121) that "richly yolked masses of mesenchymatous protoplasm become aggregated around the nerve, which till now has been quite naked." Again ('02) he writes that "in tracing back the motor trunks of the spinal nerves I reached a stage in which the faintly fibrillated trunk was ensheathed in a nucleated mass of protoplasm of mesenchymatous origin." The mesenchymatous origin of these cells has seemed so self-evident to Kerr that the problem of tracing them to their source does not seem to have occurred to him, and in consequence he advances not a particle of evidence that he has traced their genesis.

That the cells of somatic motor nerve anlagen in Squalus are largely, if not exclusively, of medullary derivation seems demonstrated by the following facts:

First, when cells make their earliest appearance in the nerve anlagen they lie partly in and partly outside of the neural tube. Then later, when cells are found definitely within the anlagen, as seen in figure 12, they appear at the base of the anlagen and near the tube. As cells grow more numerous in the anlagen in later stages more nuclei appear to be in the process of migration from the tube. As a result of the migration, the contour of the tube as seen in cross-section becomes changed and the nerve anlage greatly thickened. Furthermore, the nerve anlage shows a limiting membrane continuous with that of the tube, which makes it possible to distinguish the boundary of the nerve anlage and to infer its independence of mesenchymatous cells in the immediate vicinity. Moreover, the boundaries of the cells of the anlagen retain their smooth epithelial contour, while the mesenchymatous cells assume characteristically irregular, branched outlines. Whereas at first the cells of the sclerotome from which the mesenchyma of the region is derived, are closely apposed to the nerve anlagen, as seen in the figures on plates 1 and 2, they soon lose contact with the nerve and with each other and become metamorphosed into a loose connective tissue, but still retain

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connection with each other by fine plasmodesmatous threads. Thus the study of serial sections of Squalus embryos in closely related stages of histogenesis permits no doubt that the cells of somatic motor nerve anlagen are in large part migrant medullary elements.

From an estimate of the number of migrating medullary cells and a comparison with the estimated number in adult nerves the writer ('03) concluded that the neurilemma receives accessions in later stages from the mesenchyma and that the mesenchymatous participation in the formation of the sheaths of the adult nerve is greater than is the medullary contribution. The reasons for this inference are more convincing if, as has been suggested by Harrison ('01) and others, some of the migrant medullary elements form the sympathetic anlagen. The writer agrees with His, Jr. ('97) that at least a part of the cells of somatic motor anlagen have a mesenchymatous derivation.

8. What is the fate of the cells found in somatic motor nerve anlagen?

Three views have been advanced as to the fate of the cells of somatic motor nerve anlagen:

1. They are 'nerve-forming cells' and they secrete the neurofibrillae.
2. They form the neurilemma cells.
3. They become the ganglion cells of the sympathetic.

According to the first view the cells of somatic motor nerves anlagen form the nerves, either by fusion into cell-chains as Schwann ('39) and Balfour ('78, '81) suggested and has since been maintained by Marshall ('78), Van Wijhe ('82, '86, '89), Beard ('85, '88, '92), Beraneck ('87), Goette ('88), Dohrn ('91), Miss Platt ('94, '96), Sedgwick ('94) with modifications, Hoffmann ('96), Kupffer ('90, '91, '94), Capobianco e Fragnito ('98), Rafaelle ('00), Bethe ('00–'07) with modifications, Brachet ('05, '07), Cohn ('05–'07) and Oscar Schultze ('04, '07); or as the 'nerve cells' which secrete the neurofibrillae and which attain connections with ganglion cells and muscle fibers along plasmodesmatous paths without the participation of cell-chains.

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By his discovery of a 'ventral neural crest' in Ammocoetes Kupffer was led to abandon the cell-process theory of nerve development and to adopt the cell-chain hypothesis. According to Sagemehl ('82) and Held ('09), however, somatic motor nerves in Petromyzon are primarily fibrillar. Consequently, von Kupffer's inference may be regarded erroneous as the result of defective observation.

Schultze ('04–'07) has adopted a modified form of the cell-chain hypothesis from his observation of the growth of nerves in amphibian embryos, in which he finds the nerves primarily cellular. He consequently regards the nerves as a syncytium of peripheral neuroblasts, on the assumption that the cells are the formative ones which secrete a nerve. Thus Schultze regards the neurilemma as ectodermal in origin.

According to Held ('09), however, Schultze has failed to see the earlier stages of nerve histogenesis before the anlagen have acquired a cellular character. Held ('09) regards the cells which find their way into embryonic nerves as 'Leitzellen,' and holds that they have nothing to do with the formation of nerve fibers more than to furnish the paths in which the neurofibrils are driven forth from the neuroblasts. But Schultze claims that the fibril-free cells (Held's Leitzellen) are as much neuroblasts as muscle-forming but primarily fibril-free cells are myoblasts.

The writer ('03) argued on the following grounds that the cells of somatic motor nerve anlagen have nothing whatever to do with the formation of neuraxons:

1. In the earliest stages of histogenesis, when the number of fibers increases most rapidly in the nerve anlage, the cells of the anlage are distinctly peripheral in relation to the fibrillar bundles (Bardeen, '03, has also emphasized this point).

2. None of the ventral nerve cells at any stage of histogenesis show the deeply-staining properties of neuroblast cells such as appear in the ganglia of the dorsal (somatic sensory) nerves. Without exception the cells of the somatic motor nerve anlagen are vacuolated, granular and lightly stained.

3. While marked changes in size and shape (correlated with the growth of the neuraxons) appear in the neuroblasts of the

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sensory ganglia, no such changes appear in the cells of the somatic motor nerves.

4. While the long axes of the neuroblasts of the sensory nerves correspond, and are parallel with the direction of growth of the neuraxons, no such relation is seen in the cells of the somatic motor nerves in those early stages when the fibers increase in number most rapidly.

5. The neurofibrils do not lie within, nor are they directly connected with, the protoplasm of the cells of the somatic motor nerve anlagen. The cells in the earlier stages of histogenesis are clearly peripheral to the neurofibrillae. On the basis of such considerations, it appears extremely doubtful if the cells of somatic motor nerve anlagen have genetic relations to the nerve fibers. The cells must have some other fate.

On the other hand, Cajal ('08) thinks that he has been able to discover nerve-forming cells in a bipolar phase in the somatic motor nerves of the chick.

9. What is the histogenesis of the neurilemma?

A second, and practically unanimous opinion is that the cells of embryonic nerves form the neurilemma sheaths. Indeed, this has been the opinion of investigators, whatever their creed as to the histogenesis of nerve. According to supporters of the cell-chain theory (e.g., Dohrn, '91), that portion of the peripheral protoplasm of the nerve cells which does not enter into the formation of the neuraxon becomes the neurilemma sheath. The same opinion is shared by supporters of the process and of the plasmodesm theory. Difference of opinion centers chiefly about the problem of the origin of the cells.

Harrison ('06), on experimental grounds, concluded that the neurilemma cells of the frog are exclusively derived from the neural crest and this opinion is shared by Held ('09) who thinks that the neurilemma cells have a similar origin in Axolotl and Triton. According to Held the neurilemma cells are peripherally emigrated glia cells which have secondarily followed neurofibrillar tracts already laid down. Their source varies in different vertebrates. In Petromyzon and the Selachii the source

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is exclusively medullary. In the trout some of the cells possibly come from the dorsal ganglia, while in the Amphibia they come exclusively from this source. In reptiles, birds and mammals they appear to come chiefly from the sensory ganglia.

According to the writer ('03) the cells of somatic motor nerves of Squalus have a medullary origin. Figures 12 to 32 (pls. 23–24) show the gradual transformation of cells into the neurilemma of the adult. Since the fact is unquestioned there appears no reason for repeating the evidence upon which this conclusion is based. Bardeen ('03), Carpenter ('06), Carpenter and Main ('07), also drive the neurilemma from migrant medullary cells. Kuntz ('10) confirms this conclusion.

But is it not possible that the medullary elements contained in somatic motor nerve anlagen enter into the formation of the sympathetic? Such a fate has been claimed for them by more than one competent investigator.

10. To what an extent do the emigrated medullary elements enter into the formation of the sympathetic ganglia?

In recent years the Remak-Kölliker view that the sympathetic system is of mesodermal origin has been shared by few investigators. Onodi ('86) considered such an origin as possible for the peripheral sympathetic plexuses and both Paterson ('90) and Fusari ('90) have held the same view of the genesis of the elements of the sympathetic.

Balfour ('78) and Schenk and Birdsall ('78) led the way to the present understanding of the ectodermal origin of the sympathetic. Balfour did not decide whether the sympathetic cells were derived from dorsal or ventral roots, but Schenck and Birdsall inferred their origin from the dorsal ganglia, a conclusion since drawn by Onodi ('86), VanWijhe ('89), His ('90), His, Jr. ('91, '97), von Köllicker ('94), C. Rabl ('97), Kohn ('05, '07), Lillie ('08), Held ('09) and Marcus ('09).

Hoffmann ('00) inferred a double source of origin of the sympathetic elements as derivatives both of the dorsal and ventral roots, an opinion shared by Neumayer ('06) and Kuntz ('11).

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An exclusively medullary origin of the sympathetic elements has been inferred as a possibility by Harrison ('04) on experimental grounds, and Froriep ('07) draws the same inference. Kuntz ('10, p. 250) who had stated in an earlier paper that Froriep's conclusion "is probably correct with regard to the neurones in the sympathetic trunks and the prevertebral plexuses," in a later paper ('11) supports the view of the double source of the sympathetic elements.

Held ('09) draws the conclusion that the cells of the motor roots have nothing to do with the formation of the sympathetic system, on the following grounds: First, the anlage of the sympathetic ganglion in Selachii lies entirely in the axis of the sensory nerve root and not in that of the motor root. Second, the motor root has fewer cells, is nowhere thickened, and is nowhere united with the sensory nerve by means of cell-strands. Moreover, the ventral nerve extends along the myotome parallel with the sensory nerve, but its cellular material is not mixed with that of the latter. Also, the motor root lies lateral to the sensory root, nearer the myotome and farther from the sympathetic. The two are not united by cell-strands. Finally, the two unite ventral to the sympathetic anlage.

With Kohn and Froriep, Held admits the principle of a free cell migration of purely nervous cell clusters, in the formation of the sympathetic, but thinks that the sympathetic ganglia arise by the budding of chain-like connected cell masses and strands containing both ganglion cells and sheath cells.

Kuntz ('11) is the most recent student of the histogenesis of the sympathetic in Selachii, and his is the latest presentation of the case in favor of the medullary origin of some of the elements of the sympathetic. Kuntz's argument that the cells of the ventral roots as well as those of the dorsal participate in the formation of the sympathetic appears to consist of the following considerations: In sections of earlier stages (11 mm. Squalus embryos) scattered cells of large size and deeply staining nuclei appear in the mesenchyma between the myotome and the dorsal aorta. Because of their staining properties and evidence of cellular migration along the nerve anlagen, Kuntz assumes these

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cells to be derived from the dorsal ganglia and the ventral nerve roots. In sections of later stages (15 mm. embryos) the anlagen of the sympathetic ganglia may be seen as clusters of similar cells attached to the nerves at the level of the aorta. The deeply staining cells of the mesenchyma are now less numerous. He therefore infers that they have entered into the formation of the ganglia. Proof that the sympathetic anlagen are not the product of the continued migration of cells from the dorsal and ventral roots is not presented. As to the evidence of migration, Kuntz is able to obtain such kinetoscope effects as the following: "numerous cells (in a 10 mm. embryo) push out from the ventro-lateral angles of the neural tube and migrate peripherally along the paths of the motor nerve-roots." That such cells enter into the formation of the sympathetic ganglia he thinks is proved by the following considerations (p. 206):

> As my observations on the early stages of embryos of Acanthias have shown, numerous cells migrate peripherally both from the neural crest and from the ventral part of the neural tube before the fibers of the ventral nerve-roots can be traced peripherally to the level at which the sympathetic trunks arise. These cells later become aggregated to form the anlagen of the sympathetic trunks. In view of these facts it can not be doubted that in embryos of Acanthias many cells which have their origin in the ventral part of the neural tube enter the anlagen of the sympathetic trunks.

While there seems little reason to doubt that cells of somatic motor nerve anlagen in Squalus participate in the formation of the neurilemma, convincing evidence that they migrate into the anlagen of the sympathetic is wanting. The assertions of Kuntz in this connection appear quite unconvincing. In the numerous papers by this investigator which have appeared in rapid succession in recent years, covering the development of the sympathetic in all classes of vertebrates except amphibia, observations and conclusions, sense impressions and inferences are indiscriminately advanced as 'observations.' Kuntz, for example, does not bring forward the slightest evidence to prove the assertion ('11, p. 183) that "the cells which migrate peripherally from the neural crest and the neural tube . . . . become scattered in the mesenchyma of the region lying between the lateral mus-

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cle plates, the notochord and the aorta." The fact that some nuclei found in the mesenchyma have a more deeply staining quality certainly does not prove such an unqualified assertion. That emigrated medullary elements enter into the sympathetic is possible, but Kuntz has presented no facts that make this inference seem more certain.

So far as the evidence from sections of Squalus embryos goes, it seems rather to favor the view that the sympathetic anlagen receive their cellular elements largely if not exclusively from the sensory ganglia, as inferred by investigators upon all classes of vertebrates from Schenck and Birdsall to Held and Marcus. In the first place there appears no reason to doubt the ventral movement of the cells which enter into the formation of the dorsal ganglia. The entrance of cells into the sympathetic anlagen would involve only the continuation of this migration on the part of some of these cells. The masses of cells which constitute the anlagen of the sympathetic appear somewhat more closely connected with the sensory bundle of the embryonic nerve than with the motor bundle. Such relations appear in frontal sections at the level of the ganglionic anlagen (fig. 30).

In Squalus, however, the separation between sensory and motor bundles in the mixed spinal nerve, on the median side of which the sympathetic anlagen first make their appearance, does not appear as distinct as described by Held for other Selachii. In such sections cells lie between the sensory and motor bundles, and protoplasmic strands connect the motor bundle with the ganglia, so that the possibility that medullary elements enter the ganglia from the motor root does not seem excluded. Connection, on the other hand, by no means proves a migration. Under the circumstances inferences appear most uncertain.

But if one admit an analogy between the development of cranial and spinal somatic motor nerves, there are facts connected with the development of the oculomotor and the trochlear which favor the inference of the predominantly ganglionic origin of the sympathetic anlagen. For the first clusters of cells associated with the anlagen of these nerves are derived from the neural crest. These cell clusters, in their relations and—in the case of

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the ciliary—in their adult structure, appear to be sympathetic. Their derivation from the neural crest favors the inference that the sympathetic anlagen of the trunk have a similar origin.

It may be further urged in favor of the ganglionic origin and against the medullary derivation of the sympathetic anlagen in Squalus that the medullary migration into somatic motor nerves, like the abducens and the hypoglossus which have no sympathetic anlagen, is as striking as in those nerves associated with sympathetic ganglia. The migrant cells of the hypoglossus and abducens can have no other destination than the neurilemma. On the other hand, sympathetic cells do migrate along the vagus nerve, the ganglionic nerve of the hypoglossus segments. So the evidence seems to favor the opinion that in Squalus the sympathetic anlagen are derived from neural crest elements and not from emigrated medullary cells.

11. Summary of the histogenesis of spinal somatic motor nerves

The more important features of the histogenesis of spinal somatic motor nerves in Squalus are shown in figures 23 to 30, and may be briefly summarized as follows:

Nerve and muscle are not primarily connected with each other in Squalus embryos. Previous to the establishment of protoplasmic connection, the space normally found between somite and neural tube is filled by a vacuolated, non-staining, non-protoplasmic liquid containing a relatively small amount of coagulable material.

Protoplasmic connection of somite and tube is established by an amoeboid protoplasmic extrusion from cells in the ventrolateral wall of the neural tube forming the 'protoplasmic bridges' of Paton ('07) or 'plasmodesms' of Held ('06). The cell processes which form these connections extend gradually along the median surface of the somite between myotome and sclerotome.

Within these processes the neurofibrils soon make their appearance, as shown in Cajal and Bielchowsky-Paton preparations. This evidence demonstrates the neuroblastic nature of the cells

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which form the protoplasmic connections between tube and somite and their processes are therefore to be regarded as neuraxons.

The cell-chain hypothesis of neurogenesis receives no support from the evidence presented in sections of Squalus embryos. The neurofibrillar structure appears in the nerve anlagen before any cells are present in them.

The growth of a nerve fiber toward its terminal-organ does not involve the use and resorption of primary plasmatic paths but simply the movement and differentiation of the protoplasm of the medullary neuroblast. The most convincing demonstration of the truth of this assertion is afforded by the growth and extension of the processes of Rohon-Beard cells.

The numerous cells which, in somewhat advanced stages of histogenesis, make their appearance in the ventral nerve anlagen are not of mesenchymatous but of medullary origin; exclusively so in the earlier stages of development. That mesenchymatous cells are added to the growing nerve in more advanced stages to form the connective tissue sheaths seems probable.

The cells of the motor nerve anlagen have no genetic relations to the neurofibrils or neuraxons. In other words they are not 'nerve cells' in the von Apathy sense, nor do they unite in chains to form the neuraxons or neurofibrils with their sheaths. Whether or not they participate in the formation of the sympathetic is an open question. The evidence on the whole favors, but does not prove, the conclusion that most of the cells of the sympathetic have their source in the dorsal ganglia. That the cells of the motor nerve anlagen in Squalus for the most part form the neurilemma cells can be convincingly demonstrated.

Thus the phenomena of spinal motor nerve histogenesis in Squalus support the Kupffer-Bidder-His theory of nerve histogenesis, which has recently been strongly confirmed by the brilliant experiments of Harrison and Lewis.

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HISTOGENESIS OF THE EYE MUSCLE NERVES

Does the histogenesis of the eye-muscle nerves resemble that of spinal somatic motor nerves, and are they therefore morphologically comparable? Upon the answer to this question depend in very large degree our views of the morphology of the vertebrate head.

1. General description of the histogenesis of the eye muscle nerves

The three eye-muscle nerves make their appearance at different stages in the development of the embryo; the oculomotor in a 9.5 mm. embryo; the abducens in a 10 mm. embryo; and the trochlearis in a 19 mm. embryo. They arise like spinal somatic motor nerves as plasmatic protrusions from the wall of the brain. Their terminations are amoeboid and remain so until connection with the muscle is established. The primary anlagen possess a peripheral layer of clear protoplasm of somewhat granular structure, within which may be detected an axial deeply-stained fiber (fig. 32). The thickness of the peripheral protoplasmic sheath varies in inverse ratio with the length of the fiber. As the nerve anlage elongates the granular sheath becomes exceedingly thin. The trochlear, from the time of its first appearance, in contrast with the abducens and oculomotor, appears fibrillar rather than protoplasmic, owing to the delicacy of the plasma film surrounding the axial fibers (figs. 49 and 50). This difference may be attributed to the extended course of the fibers of the trochlear within the brain wall.

Evidence of a primary plasmatic path extending from the amoeboid terminations of the eye muscle nerve anlagen to the myotomes with which they are later connected is lacking. The demonstration of their presence or absence is rendered difficult, however, as a result of the presence of a loose mesenchyma in the spaces traversed by the elongating nerve anlagen. The anlagen assume close relations with mesenchyma cells and their processes, but so far as may be observed these connections are secondary and are independent of the process of elongation of the nerve anlagen. In all cases where it is possible to identify

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the growing tips of the nerve fibers the amoeboid terminations have no intimate relations with plasmodesms extending toward the muscle anlage, although they indisputably have more or less indirect connections with the processes of adjacent mesenchyma cells. Evidence that these connections are utilized in the extension of the nerve anlage has not been discovered, and the burden of proof rests upon those who assert the absorption of these plasmodesms into the nerve path.

The relations of the nerve fibers with bipolar neuroblasts in the somatic motor column of the brain are as easily demonstrable in Squalus embryos as in the adults and are especially clear in Cajal preparations. Even in Vom Rath preparations it is possible to follow with certainty the deeply stained processes of the neuroblasts into the roots of the nerve anlagen. There appears no good reason to doubt the genetic relation of the neuroblasts to the nerve fibers. The fact that the anlagen of the eye-muscle nerves are primarily fibrillar and not cellular, and that the cells are secondarily added to the anlagen and remain for some time distinctly peripheral in relation to the bundle of fibers, and that none of these cells assume the appearance of neuroblastic cells, constitutes evidence quite irreconcilable with the cell-chain hypothesis.

The cells which make their appearance in relation with the anlagen of the eye-muscle nerves are partly of mesenchymatous and partly of medullary derivation, like those associated with spinal somatic motor nerves. Cells are also added to the distal portion of the trochlear and oculomotor anlagen from the superficial and profundus branches of the trigeminal nerve, forming the anlage of the ciliary ganglion in the case of the former, and of a transient (?) ganglion in the case of the latter. Thus the relations to sympathetic ganglia of these two nerves seem to be the same as those of spinal somatic nerve anlagen. The abducens assumes no connections with ganglionated nerves and (therefore?) is associated with no sympathetic ganglion. Whether any of the medullary cells associated with the oculomotor and trochlear anlagen participate in the formation of the sympathetic ganglia is uncertain, as no criterion of distinction between the

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various cell elements derived from different sources has been found. The clusters of ganglion (?) cells associated with the trochlear anlage, which the writer interprets as homologous with sympathetic ganglia, are clearly derivatives of the superficialis nerve and not migrant medullary elements. Most of the cells associated with the anlagen of the eye-muscle nerves may be traced into the neurilemma cells of the differentiated nerves. Their gradual penetration into the fiber bundles of the anlagen, beginning with their proximal and distal extremities, may be easily followed in successive stages.

The nidulus of the oculomotor is limited to the somatic motor column of the midbrain vesicle (neuromere II) and presents no evidence of subdivision into two or more niduli. The nidulus of the trochlear lies in the somatic motor column of the first hindbrain neuromere (neuromere III). That of the abducens is post-otic and extends through two post-otic neuromeres (VII and VIII). These relations afford important clues to the primitive segmental relations of the eye muscle nerves, and present an insuperable difficulty to the hypothesis that the eye muscles have migrated into their present relationships from a post-otic source.

2. Does the histogenesis of the oculomotorius resemble that of a somatic motor spinal nerve?

a. Are the muscle and nerve, that is, midbrain and somite 1 of VanWijhe, connected with each other ab initio? Among the opinions in regard to the histogenesis of the oculomotor nerve no one has maintained upon an observational basis that the nerve is ab initio connected with the first somite of VanWijhe. Not even Sedgwick ('94), who regarded himself as a supporter of the Hensen theory of the primary connection of nerve and muscle, was able to maintain this view by the histogenesis of the oculomotor; for he stated that the oculomotor "is differentiated from the ciliary ganglion to the floor of the midbrain." It appears, therefore, justifiable to infer—in view of the failure of all students of this much investigated nerve to demonstrate a

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primary protoplasmic path connecting its nidulus and its end-organ—that in this respect the histogenesis of the oculomotor resembles that of a spinal somatic motor nerve as described above. The evidence about to be presented goes to show that the midbrain vesicle becomes connected with the first head-cavity by means of the movement or continuous extension of the protoplasm of neuroblasts situated in the somatic motor column of the midbrain.

There is, however, a slight difference in the conditions under which connection of tube and somite are effected as compared with those which obtain in the growth of spinal somatic motor nerves. As a result of the late appearance of the oculomotor anlage, relatively to the formation of a loose mesenchyma in the head, the region between midbrain and somite, which had been earlier filled with an unstaining plasmoid substance, becomes filled with a loose mesenchyma of uncertain origin, and protoplasmic connection of tube and somite is effected by growth in the midst of loose mesenchyma. Since it is almost as difficult to find the oculomotor anlage in the midst of this connective tissue, especially in preparations made by the older non-neurological methods, as to find the proverbial needle in a haystack, it is not surprising that the discovery of the true manner of growth of the nerve has been delayed and that difference of opinion has arisen.

Since, however, today all investigators, whose observations are sufficiently extended to cover this point, agree that midbrain and the first head cavity become connected with each other secondarily, and since the opposite view is, for this nerve, an assumption without a single drawing or demonstration to support it, there seems to be no good reason why an affirmative answer should not be given to the question: Are protoplasmic connections between somite 1 and midbrain primary or secondary? Held's ('09) assertion, that the neurofibrillae of the oculomotor always appear as intra-plasmatic fibrils, affords no foundation for inductions regarding the genesis of these protoplasmic paths. Held himself admits that he does not know whether the paths are primary or secondary.

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Gast ('09, p. 428) expresses himself as agreeing with Dohrn that primary paths do not exist for the oculomotor. His observations confirm those of Harrison ('07) that the first fiber anlagen are amoeboid and those of the oculomotor are the processes of medullary neuroblasts.

In disproof of the view that the oculomotor is primarily connected with its muscle, Belogolowy (10, p. 366) mentions the fact that in embryo chicks a transient branch of the oculomotor extends to the external rectus muscle, later innervated by the abducens. Belogolowy is unable to reconcile the presence of this transient and aberrant relationship with the doctrine of the fixed and unchangeable relationship of nerve and muscle.

According to Filatoff ('07) the oculomotor anlage appears in Emys primarily as a cellular strand extending from the myotome of VanWijhe's first somite toward the base of the midbrain. Filatoff, therefore, infers the primary connection of nerve and muscle. Johnson ('13), however, finds that in reptile embryos the anlage of the oculomotorius becomes secondarily connected with its myotome. "Filatoff's conclusions are not applicable to Chelydra."

b. What cells contribute to the formation of the protoplasmic connections between midbrain and somite 1? According to Miss Platt ('91), Mitrophanow ('93) and Sedgwick ('94) protoplasmic connection between midbrain and somite 1 is initiated by a proliferation of cells from the mesocephalic ganglion toward the brain. According to Sedgwick this migration is accompanied by a differentiation of a pre-existing syncytial strand. Ziegler ('08) also infers the centripetal growth of the oculomotor, on the basis of the evidence that in a 25 mm. embryo of Chlamydoselachus the oculomotor "has not extended its growth as far as the floor of the midbrain." Since the oculomotor nerve makes its first appearance in a 9–10 mm. selachian embryo and connection between brain and somite is already established in a 10 mm. embryo, Gast is undoubtedly correct in inferring that the oculomotor anlage in Ziegler's specimen was ruptured through shrinkage and that his inference is consequently fallacious. Miss Platt, Mitrophanow, and Sedgwick were also dealing with ad-

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vanced stages in the histogenesis of the oculomotor and they were consequently led astray in their inductions.

Filatoff's ('07) assertion that the oculomotor is differentiated from the myotome toward the brain in Emys has not been confirmed by the more recent investigation of reptile embryos by Johnson ('13). According to a second view—upheld by His ('88), Chiarugi ('97), Neal ('98), Held ('09), Gast ('09), Carpenter ('06), Belogolowy ('10)—the first protoplasmic connection between midbrain and somite 1 is effected precisely as has been found for spinal somatic motor nerves, by the continuous extension of the processes of medullary neuroblasts. Sooner or later, according to Dohrn ('88, '91), C. L. Herrick ('93), Goronowitsch ('93), Chiarugi ('97), Carpenter ('06) and Gast ('09), this protoplasmic movement is accompanied by a migration of medullary cells from the base of the midbrain. Neither Neal nor Held were able to find convincing evidence of nuclear migration into the oculomotor roots, but they did not deny the fact of migration.

The evidence presented in sections of Squalus embryos and represented in the figures of plate 6 of this paper, strongly confirms the opinion of those who have maintained the genetic relations of medullary neuroblasts in the ventral wall of the midbrain to the first protoplasmic connections between midbrain and the first somite. The anlage of the oculomotor makes its first appearance in Squalus embryos of 9 to 9.5 mm. (fig. 58), as a short, deeply-staining fiber, formed by the union of the processes of medullary neuroblasts. The evidence that this is the anlage of the oculomotor consists in the fact that the point of attachment to the brain, the direction of the long axis of the process, and the histological appearance correspond with those of the oculomotor in a 10 mm. embryo when the connection of the nerve with the myotome is already established. The nerve anlage already consists of two roots, each containing a deeply staining fiber surrounded by an envelope of granular protoplasm. At the point of union of the two roots a mesenchymatous cell appears in close proximity to the anlage. Evidence of the migration of medullary cells is wanting at this stage. The deeply staining processes of neuroblasts at the base of the midbrain

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extend toward the nerve anlage and may in some cases be traced to a point outside the external limiting membrane of the brain wall.

In later stages (fig. 59) a larger number of processes of medullary cells may be traced toward the nerve anlage and a larger number of deeply stained fibers may be seen within the roots of the anlage. In this, as in all subsequent stages, mesenchymatous cells may be seen in close proximity to the nerve fibers. Some earlier stages, such as are represented in my ('98) figures *G* and *H*, pages 222–223, show no cells whatever in relation to the oculomotor anlage; the majority of sections of these early stages show cells more or less closely associated with the nerve anlage. That these cells are mesenchymatous seems indicated by the fact that there is in these stages no evidence of medullary migration and that the possibility of a derivation from the mesocephalic ganglion is excluded, since the nerve has as yet no connection with that ganglion. No evidence of a genetic relation of these cells to the nerve is discoverable. In all respects they resemble the branched granular cells of the surrounding mesenchyma. Comparison of these with later stages in the development of the oculomotor (figs. 61, 64, 70) favors the inference that the fibers of the oculomotor are of neuroblastic origin and that they have their nidulus of origin in the base of the midbrain.

The oculomotor therefore attains connection with its terminal organ secondarily, in precisely the same manner as a spinal somatic motor nerve.

c. Have these protoplasmic connections genetic relations to the neurofibrils of the oculomotor? Most embryological investigators of the oculomotorius have paid no attention to the genesis of the neurofibrils. This is true of the latest research upon the histogenesis of the oculomotor—that of Gast ('09)—as of the earlier ones. In fact, no investigation of the histogenesis of the nerve by the use of a specifically neurofibrillar stain has been made. The vom Rath method, as applied by Neal ('98) and Carpenter ('06), comes the nearest to a truly neurofibrillar stain of any which have been used upon the nerve. Of the histological

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results of this method Carpenter ('06, p. 195) says that "a heavy black precipitate along the neuraxons differentiates these clearly against the less darkly colored stroma in which they appear to be imbedded." The appearances presented in sections prepared by this method resemble those in Cajal and Bielchowsky-Paton preparations in demonstrating, in the very earliest stages of histogenesis, deeply staining fibers within the nerve anlagen. And, while the results are not as specific and differential in vom Rath preparations, the staining is more complete than in either of the other two, so that the connection of the fibers with medullary neuroblasts is more clearly demonstrated. Now, since in vom Rath preparations there is no stage in the development of the oculomotor when such deeply stained fibers are absent from the nerve, and since the connection of these fibers with processes of medullary neuroblasts can be readily traced in many sections, and since there is not the slightest evidence that the cells associated with the fibrillar bundle of the nerve have any genetic relations with the fibers, it appears legitimate to conclude that the neurofibrils are differentiated within the processes of the midbrain neuroblasts, which, by their peripheral extension, form the protoplasmic connection between brain and somite.

Vignal ('83), Bardeen ('03), Carpenter ('06) and Paton ('09) have called attention to the coarseness of the primary fibers of embryonic nerves as compared with those seen in later stages of histogenesis and have inferred a process of splitting of the primitive fibers into true fibrils, an inference that seems to have been convincingly demonstrated by Miss Dunn ('02). The present paper makes no contribution to the discussion of this important histogenetic problem.

In the neuroblastic origin of its fibrils the oculomotor resembles histogenetically a spinal somatic motor nerve.

d. Are the neuraxons of the oculomotor multicellular in origin or are they the processes of medullary neuroblasts? The evidence that the neuraxons of the oculomotor are formed as the result of protoplasmic movement of neuroblasts in the somatic motor column of the midbrain consists, first, of the fact that the growth of the nerve is centrifugal as stated for various vertebrates by

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His ('88), Dohrn ('91), Chiarugi ('97), Neal ('98), Carpenter ('06), Gast ('09), Belogolowy ('10). Appearing at first as protoplasmic outgrowths from the base of the midbrain, the anlage of the nerve elongates in later stages in the direction of their terminal organ—the first somite—with which it quickly becomes connected.

In the second place, the nerve, in all stages of differentiation in embryonic material, manifests a fibrillation in the form of coarse, deeply-staining fibrils which appear connected with the deeply staining processes of midbrain neuroblasts. On the basis of analogy with phenomena seen in the histogenesis of Rohon-Beard cells and in preparations of the living nerve fiber in cover-glass preparations, such evidence points toward the neuroblastic origin of the neurofibrils. In no sections prepared by any of the neurological methods used, is evidence to be found of the fusion of centripetally growing fibers with processes of medullary cells in the manner suggested by Paton ('07).

Finally, the inference is further strengthened by the absence of any positive evidence in favor of the cell-chain hypothesis. It is true that cells appear along the nerve anlage from very early stages in histogenesis, but none of these cells show the familiar form and staining properties of neuroblasts. On the basis of this evidence the conclusion appears warranted that each of the neuraxons of the oculomotor is the product of one or more medullary neuroblasts and not the product of the fusion of a chain of cells. The analogy with the histogenesis of spinal somatic motor nerves is clear.

Burckhardt ('92) describes medial and lateral niduli of the oculomotor in Protopterus, confirming Ahlborn's ('84) description of the central relations of the nerve in Petromyzon. Ahlborn's assertions, however, are not confirmed by Johnston ('05) who finds the nidulus of the oculomotor to be that of a somatic motor nerve. All investigators agree that the nidulus of the oculomotor in selachians belongs in the somatic motor column.

e. By what means does increase in the length of the neuraxon take place? The oculomotor develops under conditions which differ somewhat from those which have been described for spinal

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somatic motor nerves, since the region through which it grows is filled with a loose mesenchyma before the growing tip of the nerve emerges from the base of the midbrain. Under such conditions it is difficult to ascertain that processes of mesenchymatous cells make no contribution to the growth of the nerve. The burden of proof, however, falls upon those who claim that the nerve grows by the differentiation, in situ, of plasmodesmatous paths. Such proof has not been given.

As has been suggested, the presence of a granular envelope around the fibers of the oculomotor is not to be taken as evidence of primary protoplasmic paths. Were a primary protoplasmic path of the diameter of the anlage of the oculomotor present, it could easily be found and traced in the sections. The fact is, however, that in all the stages in which the nerve anlage may be traced to its peripheral termination in the stages before it reaches the myotome, the distal end shows an amoeboid character, precisely resembling the distal extremity of nerves growing in cover-glass preparations as drawn and described by Harrison, Lewis and Burrows. No direct relation with the processes of adjacent cells nor with a direct plasmodesmatous path extending toward the myotome can be detected. All of the phenomena advanced by Held ('09) in his attempt to reconcile the Hensen with the Kupffer-Bidder-Harrison theory and to establish the assumption of primary plasmodesmatous paths are fully in harmony with the process theory of the free outgrowth of nerve fibers, while the Hensen-Held theory of primary plasmodesmatous paths finds as little support in the phenomena presented in the histogenesis of the oculomotor as in the growth of spinal somatic motor nerves.

f. What is the source of origin of the cells of the oculomotor anlage? Dohrn ('91) was the first to affirm the medullary origin of the cells of the oculomotorius anlage and his conclusions have been repeatedly confirmed by later investigators, among them Goronowitsch ('93), C. L. Herrick ('93), Chiarugi ('97), Carpenter ('06) and Gast ('09). Neal ('98) and Held ('09) were unable to find convincing evidence of, but they did not deny, medullary migration into the oculomotor. Dohrn's argument

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for his conclusion was that cells of the midbrain migrate peripherally and then send out processes, which unite in a network, just outside the base of the midbrain, to form the stem of the nerve. Immediately at the beginning of the plasma outflow, cells are seen half in and half out of the wall of the tube, and later, before the oculomotorius shows any connection with the mesocephalic ganglion, large deeply-staining nuclei, like those which appear in the process of emergence from the neural tube, make their appearance in the network of the roots of the nerve. In later stages the nuclei, in increasing numbers, appear to emerge from the midbrain into the nerve anlage. The phenomena of medullary migration into spinal somatic motor nerves add support to Dohrn's contention.

Evidence similar to that presented by Dohrn ('91) may be found in sections of Squalus embryos in stages from 10 to 15 mm., and confirms the accuracy of his description. The cells closely associated with the oculomotor in the earliest stages of development, appear to be mesenchymatous rather than medullary in origin, but it seems not unlikely that these, like similar mesenchymatous cells associated with spinal somatic motor nerves in the very earliest stages of their appearance, are not permanently associated with the nerve. Their relations may be purely topographic and transient. But there is no reason to doubt that some of the cells of the oculomotor anlage have, like those of spinal nerves, a medullary origin.

According to Hoffmann ('85), Ewart ('90), Miss Platt ('91), Mitrophanow ('93), Sedgwick ('94), Chiarugi ('94, '97), Neal ('98), and Gast ('09) cells migrate into close relations with the oculomotorius anlage from the mesocephalic ganglion. I was not sure that these cells came into permanent relations with the nerve, while Gast inferred the derivation of some of the sheath cells from them. Harrison's demonstration, through experiments upon amphibian embryos, of the derivation of neurilemma cells from the neural crest might appear to support Gast's inference, although nerve histogenesis in amphibia is not necessarily analogous in all features with that in selachians. Gast's evidence of the forward and back—centripetal and centrifugal—

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migration of cells derived from the mesocephalic ganglion along the oculomotor nerve is not very convincing.

Carpenter ('06) finds evidence of free cell migration from the mesocephalic ganglion into the loose mesenchyma and towards the oculomotor anlage in the chick. Guthke ('06, p. 43) on the other hand, asserts that the ganglion of the profundus nerve (which he erroneously calls the ciliary ganglion) has absolutely nothing to do with the oculomotorius which has no connections with the profundus ganglion in Torpedo.

Belogolowy ('10, p. 275) infers, in agreement with Carpenter ('06), that the cells, which in the chick migrate from the brain, probably participate in the formation of the motor neuroblasts of the ciliary ganglion; and he is of the opinion that neural crest cells play an important part in the formation of the accompanying cells.

Several have inferred the participation of the mesenchyma in the addition of cells to the oculomotor anlage. Indeed that has always been the orthodox assumption of the derivation of the neurilemma of the nerve. Held ('09) was in doubt as to the actual origin of the neurilemma nuclei of the oculomotor, but regards them as belonging to mesenchymatous cells of unknown origin. There can be no doubt of the close association of mesenchymatous cells in all early stages of the histogenesis of the nerve, and it seems not unlikely that they contribute to the formation of the sheath cells of the nerve. In fact Gast ('09) confirms the assertion of His, Jr., and Romberg ('90) that neurocytes migrate freely through the mesenchyma toward the nerve anlage.

Thus, in the derivation of its cellular elements, the oculomotor of Squalus resembles a spinal somatic motor nerve. Part at least of its component cells are of medullary origin; some of them may be mesenchymatous; and, finally, the nerve has close association with cells derived from a cerebro-spinal ganglion, the mesocephalic or profundus ganglion.

g. What is the fate of these cells? The fate of these cells appears even less certain than their derivation. The opinions have been expressed that at least some of the cells—whether derived

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from the midbrain or from the mesocephalic ganglion—are neuroblast cells which form the fibers of the oculomotor; that the cells of the anlage form the neurilemma; that they contribute to the formation of the ciliary ganglion; and that those which migrate from the midbrain, if not also those that are derived from the mesocephalic ganglion, have both fates.

Taking up these views in turn, we find that Dohrn ('91) is the only one who has attempted to support the cell-chain hypothesis on the basis of evidence derived from the study of the development of the oculomotor nerve, but as he has wholly repudiated ('07) the considerations which earlier led him to advocate the cell-chain hypothesis, it seems inadvisable to discuss his arguments in favor of the former theory.

Gast ('09) asserts that some of the migrant medullary cells become located in the 'root ganglion' of the oculomotor, where they become differentiated as neuroblasts, but the evidence upon which he bases his statement is far from convincing. It would seem necessary, even were one prejudiced in favor of such a view, to be able to demonstrate in its favor more convincing evidence than the presence of spindle-shaped or even multipolar cells in the cell mass which Gast calls a ganglion, especially in preparations made according to the usual embryological methods which do not differentiate the distinctive histological elements of ganglion cells. In a section made by usual embryological methods, how can Gast tell whether a spindle-shaped cell is a nerve cell or a sheath cell? Even multipolarity is no decisive criterion of a ganglion cell. Therefore, while there may be no theoretical reasons why the migrant medullary elements may not be expected to form ganglion cells, it would seem that some more critical evidence than form is to be taken as proof that such is their fate. None of the methods used in the present investigation upon Squalus embryos demonstrate the presence of neuroblasts or ganglion cells among the cells in the roots of the oculomotor. Whatever multipolar cells appear in close proximity to the nerve appear to be similar to adjacent cells of the mesenchyma.

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On the other hand, Carpenter ('06) gives convincing reasons for thinking that some of the migrant medullary cells from the midbrain participate (as a group of smaller cells easily distinguishable from the larger ganglion cells derived from the mesocephalic ganglion of the chick) in the formation of the ciliary ganglion. If this conclusion be confirmed—and this has been done by Belogolowy ('10)—it appears that at least some of the medullary cells in the oculomotorius anlage are neuroblastic.

Gast ('09) is not able to confirm Carpenter's conclusion that some of the migrant medullary elements enter into the formation of the neurilemma, but is of the opinion that the neurilemma is formed by migrant cells from the mesocephalic ganglion which travel centrad along the nerve anlage as far as the roots by which it arises from the brain and thence they migrate back again into the nerve to become the neurilemma cells. As has been stated above, Gast's evidence of this forward and back migration does not appear very convincing. Analogy with the derivation of the neurilemma of motor roots in higher vertebrates from the sensory ganglia with which they are connected does not prove such a derivation in selachians.

That the migrant medullary elements participate in the formation of the neurilemma seems to Carpenter evinced by the following considerations: "Many of these nuclei, once out on the nerve, become elongated as they move away from the neural tube," and "maintain throughout development their close proximity to the nerve fibrils." Again, the absence of evidence of the intrusion of cells from the mesenchyma is further indication of the ectodermal origin of the neurilemma. Furthermore, analogy with the differentiation of the neuroglia elements within the central nervous system points in the same direction. Finally, Carpenter was able to trace these cells through successive stages until they were, in structure and relations, demonstrably the neurilemma elements of the differentiated nerve. I reached similar conclusions ('03) for the derivation of the neurilemma of spinal somatic motor cells. The evidence appears to warrant the inference. Even Kölliker, who for years main-

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tained that the neurilemma was of mesenchymatous origin, finally became convinced ('05) of its ectodermal origin.

By tracing the histogenesis of the nerve through closely connected stages until adult conditions are established in Squalus it is possible to demonstrate that a large number, if not all, of the cells present in the anlage of the oculomotor become differentiated as neurilemma cells. Some of these stages are shown in the figures of plate 8 of this paper.

The cells, which are at first peripheral to the bundle of fibers (fig. 65), soon begin to penetrate among them (fig. 68) as stated by Vignal ('83), Gurwitsch ('00), Bardeen ('03), Carpenter ('06), and Gast ('09). Gast is probably correct in asserting the centrifugal migration of the group of cells clustered about the roots of the nerve anlage (figs. 64, 70) and their penetration into the bundle of fibers. In fact the penetration of the fiber bundle appears to occur largely in this manner, as stated by Gast.

Altogether the evidence goes to show that the neurilemma of the oculomotor has a similar derivation and differentiation to that of somatic motor spinal nerves.

h. What is the histogenesis of the neurilemma? Gast ('09, p. 428) summarizes the histogenesis of the neurilemma of the oculomotor as follows: In its proximal portion the oculomotor passes through four different developmental stages: (1) the naked processes of the central neuroblasts extend to the mesocephalic ganglion; (2) from the mesocephalic ganglion neurocytes (Kupffer '90) wander centrad along the fibrillar bundle; these lie upon and between the fibers and form about them, especially among the roots, a loose plasmatic network; (3) the neurocytes arrange themselves wholly on the surface of the nerve anlage, which at this stage consists of a central fibrillar bundle with a cellular sheath; (4) the neurocytes migrate back into the central fiber bundle and are transformed into sheath cells.

The results of a former ('98) and of the present study are in essential agreement with this description of Gast. The evidence derived from a study of Squalus embryos, however, seems hardly to justify the inference of a forward and backward migration of neurocytes along the nerve anlage. Moreover, it

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appears to favor the conclusion that the cell clusters at the roots of the nerve anlage are of mesenchymatous and medullary derivation. The inference that cells derived from the mesocephalic ganglion migrate centrad as far as the roots of the nerve anlage does not appear to the writer to be well established. In agreement with Gast, however, I find that penetration of the fibrillar bundle begins at proximal and distal extremities of the nerve anlage, where it divides into roots and peripheral branches, and the penetration proceeds in opposite directions towards the middle stretch of the nerve. In the phenomena presented in the histogenesis of the neurilemma there appears to be no essential difference between that of the oculomotor and a spinal somatic motor nerve. In both cases the derivation of the neurilemma cells appears to be the same.

i. To what an extent do the emigrated medullary elements go to form the sympathetic? That a ciliary ganglion is associated with the oculomotor nerve in selachians seems proved by the consensus of opinion of investigators on the basis of anatomical, histological, and embryological evidence. Anatomical evidence of its presence has been presented by Schwalbe ('79), Jegorow ('86-87), and Allis ('02); on the basis of histological structure by Haller ('98); and on embryological grounds by Van Wijhe ('82), Beard ('85), Ewart ('90), Dohrn ('91), Miss Platt ('91), Hoffman ('99), Gast ('09). Physiological evidence of a functional ciliary ganglion in selachians is wanting.

Furthermore, that the ciliary ganglion belongs morphologically and physiologically with the sympathetic system has been held by many investigators since its discovery in man by Schacher (1701) and the suggestion of its sympathetic character by Arnold ('31). Later, doubt as to its sympathetic nature was raised by Schwalbe ('79), who became an exponent of the view that it is a cerebro-spinal ganglion and who initiated the long controversy regarding its nature which has not yet been ended. Carpenter ('06) has so admirably reviewed the literature dealing with this problem that it appears unnecessary to enter into an extended discussion of the various arguments for and against its cerebro-spinal character. That the ciliary ganglion is, in part

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at least, sympathetic in all forms from fishes to man seems, on the basis of anatomical, histological, embryologidal and physiological evidence, indisputable. But the presence of bipolar ganglion cells, like those of cerebro-spinal ganglia, in the ciliary ganglion of many vertebrates has led to the general acceptance of the view of its double nature, a view first advanced by Krause ('82).

But the presence of bipolar ganglion cells within the ciliary ganglion by no means demonstrates its morphological comparability with cerebro-spinal ganglia, since ontogenetic evidence shows that the entire ganglion—whether derived from the midbrain or the mesocephalic ganglion—has not a genetic but merely a secondary relation to the anlage of the oculomotor, a fact emphasized by Gast ('09).

While Dohrn ('91) claimed an exclusively medullary derivation of the ciliary ganglion in Selachii, Gast ('09), working upon the same material—in fact the same sections—concludes that they are exclusively derived from the mesocephalic ganglion. These diametrically opposite conclusions indicate how obscure the phenomena of migration are in sections of embryonic material. Carpenter ('06), working upon chick embryos, infers a double derivation of the cells of the ciliary ganglion.

Von Kupffer ('95), Johnston ('05), and Belogolowy ('10b) have attempted to associate the ciliary ganglion genetically with the 'thalamic nerve.' Johnston says (p. 244) that "since the profundus ganglion is distinct from the ciliary and is formed from a different part of the neural crest, it seems altogether probable that the ciliary ganglion permanently represents the N. thalamicus." Belogolowy's discovery of an anastomosis between the oculomotor nerve and the transient ganglion of the 'thalamic nerve' likewise seems to him to prove the homodynamy of the latter with the ciliary ganglion of vertebrates. In drawing this conclusion Belogolowy fails to take into account the fact that the ciliary ganglion of vertebrates is a derivative of the mesocephalic or profundus ganglion. It is not at all clear that the complicated anastomoses between the branches of the eye-muscle nerves in reptile embryos and their peculiar relations with branches of the trigeminal nerve

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throw any light upon the primitive relations of these nerves in vertebrates. Johnston's inference is fallacious since his premise is incorrect. The cells of the ciliary ganglion of Squalus are proliferated from the medial surface of the profundus ganglion. It may be granted, however, that the demonstration that the 'thalamic nerve' represents the primitive root of the profundus nerve, would associate this so-called nerve with the ciliary ganglion as its sympathetic visceral sensory component.

Sections of Squalus embryos give convincing evidence of cellular migration, both from the midbrain and from the mesocephalic ganglion, into or towards the oculomotor anlage, but it is impossible to feel convinced that the migration of the medullary cells extends as far as the ciliary ganglion. In fact the evidence of the participation of medullary cells in the formation of the sympathetic is as doubtful in the case of the oculomotor as in the case of spinal somatic motor nerves. The possibility of such a derivation can not be denied, but positive demonstration on the basis of evidence obtained from serial sections has not yet been given. In this respect, that is, in the derivation of its proper sympathetic ganglion, the oculomotor resembles a spinal somatic motor nerve.

j. Summary of the histogenesis of the oculomotor and of the ciliary ganglion. In all essential respects, the oculomotor nerve resembles in its histogenesis a spinal somatic motor nerve, i.e., in its appearance as a product of the protoplasmic movement of medullary neuroblasts situated in the somatic motor column of the neural tube; in its secondary connection with a mesodermic somite, Van Wijhe's first; in the growth and extension of its fibers by the continuous movement of the protoplasm of medullary neuroblasts; in the differentiation of its neurofibrils within the protoplasm of these processes; in the migration of medullary cells into the nerve anlage to form—at least in part—the neurilemma; in the probability of the participation of mesenchymatous cells in the formation of the neurilemma; in its union with cells of a cerebro spinal ganglion; and finally in its association with a sympathetic ganglion, the ciliary, derived mainly if not exclusively, from a cerebro-spinal ganglion as a result of cellular migration.

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3. Does the histogenesis of the trochlearis resemble that of a somatic motor spinal nerve?

a. Are protoplasmic connections between myotome 2 and hindbrain primary or secondary? The distance between the point of emergence of the trochlearis fibers and the myotome which this nerve innervates is, in Squalus embryos, the greatest traversed by any motor nerve. This fact lends especial interest to the development of this nerve in relation to the problem of the existence of primary paths or connections between nerve center and the end-organ. This nerve would seem to afford a critical test of the truth or falsity of the Hensen-Held hypothesis of nerve histogenesis. If any nerve in the vertebrate body needs a primary path so that it may not go astray, that nerve is the trochlear. In view of this fact it is somewhat surprising that Paton ('07), who supports this hypothesis, concedes that the trochlearis (and also the oculomotor) acquires its connection with the superior oblique muscle without the participation of plasmodesmatous bridges (Paton '07, p. 556).

Some years ago ('98, p. 237) I expressed the opinion that "the possibility of a primary connection between muscle and nerve appears excluded in the case of the superior oblique muscle and the trochlear nerve" and Dohrn, later ('07, p. 410), said quite as emphatically that "Jede Möglichkeit eines uranfanglichkeit Zusammenshangs zwischen Muskelzelle und Nervenzelle ist dabei ausgeschlossen." Belogolowy ('10a, p. 380) also agrees in affirming the absolute impossibility of a primary connection between nerve and muscle in the case of the trochlearis. While Sewertzoff ('98) and Fürbringer ('02) are unable to agree with this assertion of mine, they advance no arguments in its rebuttal. It is a significant fact that none of the supporters of the Hensen hypothesis have been able to demonstrate a primary protoplasmic path connecting the isthmus or the hindbrain with the myotome of Van Wijhe's second somite.

On the contrary, and in support of the view that the trochlear nerve develops in accordance with the process theory of neurogenesis and that the connection of hindbrain and superior oblique

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muscle is secondary, Dohrn ('07, p. 416) advances the following argument:

The development of the trochlearis forms a crux for the Hensen-Gegenbaur-Furbringer hypothesis of the primary connection of the nerve and its terminal organ. So long as we have to do with the connections of spinal somatic nerves with somites already formed, one may believe in the existence of plasma bridges and be willing to recognize in them at least the paths that guide the growing nerve. The separation in this case between tube and somite is the least possible and few cells lie between them. But if one extend this view to the eye muscles he at once meets insuperable difficulties. All these have a considerable distance to traverse in reaching their end-organ, and the abducens, oculomotorious and trochlearis solve the problem each in its own way. I have already pointed out ('01) that this theory must be tested, not on the spinal somatic nerves, but on the eye muscle and splanchnic motor nerves, if it is to be regarded as tenable, and I must now put the question to the defenders of the Hensen theory how they conceive of the connection of the trochlearis through plasma bridges with its terminal organ in the other antimere.

In embryos of 12 to 18 mm. the actual trochlearis fibers remain either completely within the neuroblasts from which they are to arise or they have at most made their way through the medullary wall to the chiasma, but are not yet protruded from the wall. The superior oblique muscle, on the other hand, has developed from the mandibular somite as the most dorsal of the eye muscles and has already begun to differentiate muscle fibers. What and how many plasmodesmatous connections must be assumed in order to establish the most complicated of all paths traversed by any motor nerve? How is one to demonstrate that first plasmodesms of the neural tube, then others of the mesenchyma, then—in case 'Kettenfasern' are present before the trochlearis fibers extend through their region of distal distribution—plasmodesms of the 'Kettenfasern,' and finally those of the muscle fibers of the superior oblique muscle are likewise prepared to furnish neurofibrils through further differentiation? Would this be in the least more easily conceivable than the outgrowth of the nerve from its neuroblasts to its terminal organ? It is true that the outgrowth points to problematical forces, but shall we be without a riddle if we put another in its stead—one that presents a number of unfounded assumptions?

Held ('06), who admits the insufficiency of the hypothesis of plasmodesmatous paths for the trochlearis nerve, thinks that he may assume as the direct path-determining impulse for the outgrowing neurofibrils the principle of the axial position of the neuroblast and that of the shortest distance. These obviously fail

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in their application to the growth of the trochlearis. The chief axes of the neuroblasts which form the trochlearis fibers do not point toward the end-organ, neither do they follow the shortest possible course, but practically the most indirect route possible.

In Squalus embryos, previous to the first appearance of the trochlear anlage, the region of its future path is filled with a loose mesenchyma derived at least in part from the neural crest. It is a most important fact, demonstrated by the observations of Kastschenko ('88), Neal ('98) and Dohrn ('07), that, from the time of its first appearance to the time it attains connections with the superior oblique muscle, the trochlear anlage in some selachians shows no close associations with mesenchymatous cells, but extends as a loose bundle of fibers through vacuolar spaces (fig. 49). The trochlearis development, says Dohrn ('07, p. 413) "affords a proof that an elongated motor nerve can grow through a considerable extent of tissue without becoming attached to a single cell of the surrounding mesoderm." Evidence of a granular protoplasmic envelope surrounding the fibers, however, is not lacking, but there is no evidence that surrounding mesenchymatous cells contribute to the production of this. The descriptions of Froriep ('91) and Miss Platt ('91) relate to more advanced stages in the histogenesis of the trochlear than those described, so that their assertions of the participation of cells in the formation of the trochlearis anlage have no relevancy in connection with the problem of the formation of the primary connection between tube and myotome.

b. What cells participate in the formation of these connections? The fact that in the adults of all classes of vertebrates the fibers of the trochlearis may be traced in suitable preparations to a nidulus in the somatic motor column, posterior to the midbrain leads to the supposition that these cells are genetically related to the fibers. The further evidence that during the period of extension of the fibers toward their terminations in the superior oblique muscle, no cells which may be regarded as neuroblasts or 'nerve-cells' in the Apathy sense, may be seen in connection with the peripheral stretch of nerve anlage, points in the same direction. The connections with cell-clusters or fragments of

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the neural crest as described by Hoffman ('89), Oppel ('90), Dohrn ('91), Miss Platt ('91), and Froriep ('91) are secondary and do not appear in the primary fibrillar stretch of the nerve anlage. Filatoff ('07, p. 358) agrees with the writer ('98) that the so-called primary trochlearis (Miss Platt '91) has no genetic relation with the definitive trochlearis, which develops wholly independently of the neural crest and of the trigeminal nerve, although it requires secondary connections with the latter. According to Belogolowy ('10a) no ganglion is associated with the trochlear in bird embryos, while in the turtle the so-called ganglion of the trochlearis has no connection with the trochlearis but is connected with the superficial branch of the trigeminal (p. 424). The same is true also of the relations of the ganglion in the sturgeon. The superficialis nerve is, therefore, to be regarded as the dorsal nerve of the trochlearis metamere.

Schwalbe ('79, '81), Johnson ('05), and Carpenter ('06) have asserted that the neuroblasts which form the nidulus of the trochlear are situated in the somatic motor column of the midbrain and not in the hindbrain. Such divergent opinion may possibly be explained by the fact that in the ventral portion of the brain in this region no constriction is present such as that which divides midbrain and hindbrain regions dorsally, so that it is difficult to distinguish the limit of these two brain divisions. The majority of investigators find the nidulus of the trochlear, either in the hindbrain or in the isthmus. The assertion of Martin ('90), that the nidulus of the trochlear is primarily in the visceral (lateral) column, and that it secondarily migrates mediad, has not been confirmed and, like many of the other amazing assertions of this writer, should be placed in quarantine as suggested by Dohrn ('07). In Squalus the nidulus of the trochlear is clearly ventral and, while the fibrillar bundle of the nerve emerges dorsally from the brain wall in the region of constriction between midbrain and cerebellum, the central fiber-tract with which it is connected may be traced posteriad and ventrad to the nidulus in the somatic motor column in the anterior portion of the cerebellar neuromere (neuromere III). On the other hand, Van Walkenburg ('10) finds two trochlear niduli in human embryos.

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Belogolowy ('10a, p. 367-8) describes the histogenesis of the trochlear, which may be summarized as follows: The first developmental stages of the nerve take place in the brain. Here the fibers of the brain are gradually differentiated as processes of cells in the somatic motor column of the hindbrain. The fibers grow in the direction of the dorsal side of the brain and toward the constriction between second and third brain vesicle, that is toward the basis of the cerebellum anlage. The fiber bundles may be easily traced through the brain wall and usually number three.

At the time when these bundles have reached a point about two-thirds the height of the neural tube a nidulus of large ganglion cells makes its appearance at the place of the future point of emergence of the fibers. The evidence of their ganglionic character consists in their larger size and in the outgrowth of fibers from them. (Belogolowy's figures, however, do not bear out the latter assertion.) This dorsal nidulus is gradually enclosed by the spongiosa and penetrated by the coarse fibers of the trochlear until only isolated cells remain scattered in the region of the chiasma. The bundle of fibers of the nerve anlage is at first free of accompanying cells, which appear first at about the level of the middle of the brain wall.

Belogolowy then goes on to present evidence that the accompanying cells can have nothing to do with the genesis of the fibers of the trochlear. Notwithstanding the divergence in his account in regard to the existence of a dorsal nidulus, Belogolowy does not hesitate to compare the trochlear with typical somatic motor nerves. He agrees with the conclusion that connection between hindbrain and superior oblique muscle is secondary, an inference which—in the light of the evidence now in our possession—there seems no good reason to doubt.

c. Have these protoplasmic connections a genetic relation to the neurofibrils? As first stated by Kastschenko ('88, p. 465) the trochlearis, from the time of its first appearance, is a fibrillar structure. In preparations of Squalus embryos by the Vom-Rath method these fibers are deeply-staining and highly refractive threads, contrasting strongly with the protoplasm of the ad-

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jacent mesenchymatous cells between which they lie. In cross sections of the nerve anlage (fig. 52, p. 181) the fibers appear as black dots or granules scattered in a granular and vacuolated protoplasmic envelope. Their appearance is essentially the same in VomRath preparations as in preparations by the Cajal or the Bielchowsky-Paton methods. The identity of this bundle of fibrils with the trochlearis in advanced stages of differentiation is established, not only by its fibrillar structure, but by its relations with tube and myotome at this and all subsequent stages of development. As this anlage has been traced in unbroken continuity until the differentiation corresponds essentially to that of the adult nerve there is no good reason to doubt the identity of the fibers of the anlage with those of the adult and that the neurofibrillae make their appearance within them. It is true that the splitting of the fibers of the nerve anlage into the neurofibrils of the fully differentiated nerve is a matter of inference rather than one of direct observation, yet students of nerve histogenesis have not hesitated to make this inference which has been drawn by Bardeen ('03), Carpenter ('06) and Paton ('07), on the ground that, while the primitive fibrils of the nerve anlage are relatively coarse structures, the neurofibrillae of later stages are much finer and more numerous. There is no reason for inferring that the neurofibrils have any other origin than the coarser fibrils of the nerve anlage, which make their appearance in the nerve from its first inception in the stages when the nerve anlage is wholly free from cells. Furthermore, at no time in the histogenesis of the nerve is there any indication of a genetic relation of the cells, which later make their appearance in the nerve, to the fibers. No neuroblasts have been discovered within the nerve anlage. So that there seems to be no reason why the histogenesis of the neurofibrils of the trochlearis may not be regarded as in every respect similar to that of the neurofibrils of spinal somatic motor nerves. In other words they are to be regarded as the product of differentiation within the neuraxon processes of medullary neuroblasts situated in the somatic motor column of the neural tube.

Miss Platt ('91a, p. 96) inferred the neuroblastic origin of the fibers of the proximal portion of the trochlearis on the basis of

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the evidence that "the fibrous root of the nerve cannot be composed of prolongations from the distal cells (derived from the R. ophth. sup. V), because the fibrous or proximal part of the trochlearis arises before the distal or cellular part; further, the fibrous root is the thickest as it comes from the brain, becoming gradually attenuated as it proceeds into the mesoderm." Belogolowy ('10a) likewise finds the trochlear of the chick fibrillar from the time of its first appearance. There appears no good reason to doubt that the trochlear anlage is not only 'fibrillar' but 'neurofibrillar' in the Apathy sense of the word.

d. Is a neuraxon of the trochlear anlage multicellular in origin or the process of a single medullary cell? While it is practically impossible for any particular neuraxon of any nerve to give an answer to this question upon the basis of direct observation (and for the trochlear nerve the difficulty is increased by the extended intra-medullary course of the fibers of the nerve) it is easy to disprove the assertion that the trochlearis anlage in its peripheral stretch is the product of the fusion of a chain of 'nerve' cells, since in Squalus, as in Pristiurus (Dohrn '07), the nerve anlage may be traced as a bundle of fibers, devoid of cells or nuclei, from its point of emergence from the brain to its terminal organ. If such evidence could convert Dohrn ('07) from the advocacy of the cell-chain hypothesis of neurogenesis which on the basis of evidence partly derived from the study of the same nerve he had defended for years, it would seem that little argument would be needed to convince unprejudiced students that the trochlear nerve develops by the free outgrowth of medullary neuroblasts. It appears unlikely that any student of neurogenesis will demand that a neuraxon be traced from neuroblast to muscle fiber in order to convince him of the applicability of the process theory to the phenomena of histogenesis of the trochlear. So that, while in the case of the trochlear nerve it is impossible to deal with individual cells and fibers, the fact that, from the time of its first appearance as a fiber bundle emerging from the dorsal wall of the brain, these fibers may be traced centrally to their connection with a group of deeply stained neuroblasts lying in the somatic motor column of the hindbrain, and that these are also the adult re-

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lations, will seem to most students sufficient evidence to demonstrate their neuroblastic derivation.

The evidence that in early stages of histogenesis the distal fibers of the trochlear are associated with cell clusters or ganglia, as shown by Dohrn and others, affords, as stated above, no support to the cell-chain hypothesis, since these connections with the trochlearis fibers are secondary. Their relations with the trochlear anlage therefore must receive another than a genetic interpretation. Such another interpretation is given below.

e. By what means does the increase in length of the neuraxon take place? The histogenesis of the trochlearis affords no evidence in support of the Hensen-Held contention of the differentiation in situ of plasmodesmatous paths in the formation of a nerve anlage. The loose distal brush of fibers (fig. 49), in which the nerve anlage terminates in early stages, show no such relations to cells or cell processes as Held's position would require. Furthermore, while the existence of a loose brush of fibers may readily be interpreted as an advantage to a bundle of neuraxons which effect connection with their terminal organ by a process of free outgrowth, there would appear to be no meaning to the phenomenon were the Hensen-Held hypothesis correct. As soon as the connection with the myotome is effected by the fibers, they quickly unite into a compact bundle and lose their brush-like form. Therefore, while it is difficult to demonstrate the free-growing terminations of the fibers within the mesenchyma, the positive evidence, as far as it is known, is in harmony with the process theory. The assertion that the trochlear is differentiated in situ through the use and incorporation of primary plasmodesmatous paths is wholly unfounded.

f. What is the source of the cells of the trochlearis? Somatic motor spinal nerves derive their cells from the neural tube by migration along the nerve anlage, possibly from the mesenchyma, and come into close association with cells masses derived from the spinal ganglia. Do the cells associated with the trochlearis anlage have a similar derivation?

That medullary elements enter the trochlear anlage has been held by Dohrn ('07) on the basis of evidence similar to that pre-

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sented in figure 53, which shows nuclei half in and half out of the brain wall at the point of emergence of the trochlearis root. Dohrn (p. 293) also called attention to the fact that the nuclei are not peripheral in position but lie between the fibers of the nerve root. Furthermore, medullary nuclei lie nearer the periphery of the brain wall in the region where the fibers of the trochlear enter the brain than they do elsewhere in the vicinity of the root, and, as development goes on, an increasing number of nuclei appear among the fibers of the nerve root. More convincing evidence of migration would be difficult to find in sectioned material.

Belogolowy ('10a, p. 375) suggests that the absence of accompanying cells in the fiber bundle of the trochlear anlage in its intracerebral and in its proximal extent proves that the accompanying cells are not medullary in origin. However, had Belogolowy studied somewhat more advanced stages with this problem in mind, it is posssible that he would have found evidence of medullary migration. The writer ('98), on grounds similar to those advanced by Belogolowy, concluded that medullary elements were absent from the trochlear anlage of Squalus, but renewed investigation of more advanced stages proves this inference to be erroneous.

On the other hand, evidence that mesenchymatous cells attach themselves to the nerve anlage is difficult to obtain and positive proof is altogether wanting. Belogolowy ('10a) infers the participation of mesenchymatous cells in the formation of the neurilemma of the trochlear. The most convincing evidence that may be secured is possibly that mesenchymatous cells lie in various degrees of proximity to the nerve anlage (fig. 51). In other words the evidence of the participation of the mesenchyma in forming the cellular elements of the nerve anlage are quite as obscure as in the case of spinal somatic motor nerves.

Miss Platt ('91) was the first to observe evidence of migration of cells from the anlage of the superficial branch of the trigeminal into or towards the trochlear anlage. The evidence is similar to that seen in the relations of the oculomotor to the profundus ganglion. Miss Platt, after describing (p. 95) the first appearance of the trochlearis as a "small fibrous nerve growing

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from the constriction between midbrain and hindbrain," says that "soon after the appearance of this small nerve, which is the root of the permanent trochlearis, cells are proliferated to meet it from the ganglion cells that lie above the superior oblique muscle." These cells cannot rise from the brain, since "no cells are found in the root of attachment." Thus the permanent trochlearis arises from two sources from the brain and from the ganglion cells."

Dohrn ('07) also inferred that the first cells connected with the trochlear anlage in Pristiurus are derived from the ramus superficialis V, while in those forms in which, as in the Torpedinidae, the superficial branch is not differentiated, but is represented by fragments of the neural crest, the trochlearis anlage acquires relations to these cell clusters, similar to those in Squalus and Pristiurus, and presents similar evidence of cellular migration toward the nerve anlage.

The evidence of cell migration from the R. superficialis V into the trochlear anlage in Squalus consists of the fact that cells appear primarily, not in the proximal root of the nerve nor in the bundle of fibers, but in the distal portion of the nerve in the region where its fibers cross those of the superficialis. The phenomena presented are practically identical with those described for the oculomotor in its cellular relations with the R. prof. Trig. As development proceeds, cells increase in number in the region between the two nerve anlagen, although the proximal portion of the nerve remains free from cells. Finally, cells accumulate between the trochlear and superficialis anlagen in a mass precisely comparable to the anlage of the ciliary ganglion, forming the cell cluster to which Miss Platt ('91, p. 100) refers as the ganglion of the trochlearis lying above the superior oblique muscle anlage.

Further evidence of migration into the trochlear anlage from the superficialis nerve is found in spindle-shaped cells closely applied to the fibers of the trochlear anlage in stages when cells are wanting in the proximal portion of the nerve and when evidence of additions from the mesenchyma is lacking. Similar spindle-shaped cells show connections, on the one hand with the ramus

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superficialis, and on the other with the fibers of the trochlear anlage.

Thus, in the derivation of its cellular elements, the trochlear resembles the oculomotor and spinal somatic motor nerves. There is no reason to doubt the medullary derivation of some of its cells; mesenchymatous participation is somewhat doubtful; and, finally, the migration of cells from a ganglionic nerve in relation with its anlage appears unquestionable.

g. What is the fate of these cells? Dohrn ('07) makes the interesting suggestion that the manner of development of the fibers of the trochlearis in Pristiurus is a natural experiment, confirming Harrison's ('04) experimental demonstration of the origin of the neurilemma in amphibian somatic motor nerves from the neural crest. That is, he concludes that the cells which migrate from the superficialis into the trochlear anlage form the cells of the neurilemma. The possibility that they may be compared with the cells of sympathetic anlagen does not seem to have occurred to Dohrn. Miss Platt ('91) speaks of these cells as ganglion cells although she has made no attempt to follow their fate in later stages.

However, the similarity of the cell-cluster, associated with the trochlearis anlage and derived from the superficialis, with the ciliary anlage in its relations to the oculomotor and the profundus is so striking that the suggestion that in this mass we have a sympathetic ganglion seems permissible. The main objection to such a view, and one that may appear insuperable, is that the trochlear appears in the adult to be associated with no sympathetic ganglion. The ganglion of the trochlear anlage—not to be confused with the fragments of the neural crest associated with the trochlear anlage in the Torpedinidae and reptiles—is conspicuous in Squalus embryos of 25 mm. but has disappeared as a mass of cells in 45 mm. embryos. Since, however, many of the sympathetic anlagen of spinal somatic motor nerves similarly disappear in these stages and do not appear in the adult, the disappearance as a distinct cell-mass of the hypothetical sympathetic ganglion of the trochlear is not to be regarded as a serious objection to the hypothesis. Moreover, the possibility

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is by no means excluded that sympathetic cells are associated with the adult trochlear nerve. This point needs investigation. The important fact remains that a cell cluster, associated with the embryonic trochlearis, has the same relations and derivation as the sympathetic anlagen of the trunk and as the ganglion of the oculomotor and that in this respect as in others the nerve conforms in its histogenesis with that of a typical somatic motor nerve.

h. What is the histogenesis of the neurilemma of the trochlear? More convincingly than any other nerve in the vertebrate body the histogenesis of the trochlear anlage shows that a nerve may become connected with its terminal organ without the slightest indication of the participation of a single peripheral 'nerve cell' or chain of nerve-forming cells. Dohrn ('07, p. 411) states that it was the study of the histogenesis of the trochlearis which converted him from a supporter of the cell-chain hypothesis to one of the process theory of His. There appears in Pristiurus (Dohrn) and in Squalus the decisive evidence which, in normal embryos, effectually invalidates the cell-chain hypothesis in whatever modified form it may present itself. The evidence is wholly convincing that the neurilemma cells of Squalus have a secondary and exogenous derivation. Primarily, instead of a cell-chain extending from nerve center to end-organ the trochlear nerve appears as a fibrillar bundle. Into this fibrillar anlage cells migrate from the neural tube and from the ramus superficialis V. Some cellular additions may come from the adjacent mesenchyma. These cells, generically independent of the fibers, soon assume an elongated form and a relation to the nerve fibers which marks their destination as neurilemma cells.

i. To what an extent do the emigrant cells go to form the sympathetic? The absence of any positive evidence of sympathetic cells in the adult trochlearis would appear to afford presumptive evidence against such a fate for any of the cells of the trochlear anlage. But the fact that sympathetic anlagen disappear ontogenetically in many spinal somatic motor nerves makes the supposition that the trochlear possesses a transient sympathetic ganglion seem not unreasonable. Moreover, until it has been

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demonstrated that sympathetic cells are wanting in the adult trochlear, the possibility that the cell cluster associated with the nerve in 25 mm. embryos forms a diffuse sympathetic along the nerve in the adult is not excluded. As far as it goes, the evidence favors the opinion that a transient sympathetic ganglion, derived from the ramus ophthalmicus superficialis trigemini is associated with the trochlear anlage as in the case of certain anterior spinal nerves. There is no evidence whatever that migrant medullary elements enter into this hypothetical transient sympathetic anlage.

j. Summary of the histogenesis of the trochlear nerve. In the manner of its growth and extension to form a secondary connection with its myotome through the protoplasmic movement of medullary neuroblasts; in the source of derivation of its neurilemma; and in its relation to a ganglionic nerve and to a sympathetic anlage, the histogenesis of the trochlear resembles in all essentials that of spinal somatic motor nerves. To this extent its serial homology with them is demonstrated.

4. Does the histogenesis of the abducens resemble that of a somatic motor spinal nerve?

a. Are protoplasmic connections between hindbrain and myotome 3 primary or secondary? No investigator has attempted to support the Hensen hypothesis of the primary connection of nerve and muscle on the basis of the histogenesis of the abducens nerve. On the contrary all who have made a careful study of its histogenesis—Dohrn ('90, '91), Neal ('98), Carpenter ('06), and Belogolowy ('10)—agree that, at first, the abducens is not connected with the posterior rectus muscle, but in its early stages of development terminates freely in the mesenchyma at the base of the brain. No evidence of the participation of plasmodesmatous paths in the forward extension of the nerve has been advanced. And, while no thorough investigation of its development from the standpoint of the Hensen hypothesis has been made, it does not seem likely that demonstrable plasmodesms would have remained unperceived.

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The mere presence of a loose mesenchyma in the region later traversed by the nerve anlage gives no presumption in favor of view of Hensen and Held. The possibility of the utilization of such material in the elongation of the growing nerve may readily be granted, but as yet no demonstration of such use of protoplasmic bridges has been made. On the contrary, it is possible to demonstrate in sections the free growing end of the nerve anlage and to ascertain, on the basis of actual observation, that no plasmodesm or undifferentiated protoplasmic path connects the end of the nerve anlage with the myotome. Such a growing end of the abducens is given in fig. 35, which shows on what slight evidence the hypothesis of the utilization of protoplasmic paths depends. The amoeboid terminations of the nerve fibers (neuraxons) show attenuated connections by means of fine granular threads—as seen in sections—with amoeboid processes of mesenchymatous cells. But such evidence, so far as it permits any inferences at all, favors the opinion that the fine amoeboid processes of the growing tip are derivatives of the nerve anlage itself. For, if the processes of the mesenchymatous cells are genetically related to them, there is equally good ground for thinking that the processes which extend from the end of the nerve anlage in all directions are derivatives of the nerve itself. Harrison's experimental results verify this assumption, since, in his preparations of the living nerve fibers, similar delicate extensions of the amoeboid termination of the nerve make their appearance. In such preparations there can be no question of the genetic relations of the fine threads. To call them paths as Held ('09) has done is obviously a misnomer for structures which radiate in all directions. Were a growing structure to depend upon such flimsy paths for the material for its growth, its extension would be neither fast nor far. Furthermore, neither this section nor others, in which the observer may feel confident that he is dealing with the actual termination of the growing nerve anlage, is the relation of the termination to adjacent mesenchymatous cells such as to suggest the utilization of their substance in the elongation of the nerve.

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In view of the unanimous agreement of all investigators of the histogenesis of the abducens that the nerve becomes secondarily connected with its myotome, and in view of the entire absence of evidence of primary plasmatic paths within which the neuraxon might be differentiated; furthermore, in view of the fact that it is possible to demonstrate the growing tip of the abducens anlage as an amoeboid structure similar to those seen in Harrison's cover-glass preparations, there appears little reason to doubt that the abducens acquires a secondary connection with its myotome. This inference is strengthened by Belogolowy's discovery that some fibers of the abducens anlage of the chick extend in their growth farther than the anlage of the posterior rectus muscle and later atrophy. It seems easier to harmonize such evidence with the hypothesis of the free outgrowth of nerve fibers than with the hypothesis of primary connection of nerve and muscle. Moreover, the fact that the nidulus of the abducens is about equidistant from post-otic and pre-otic myotomes and that, in early stages of development, its fibers grow in both directions—that is, both anteriad and posteriad—suggests that the direction of growth is chemotropically determined. The extension posteriad is, however, transient, the posterior process is soon withdrawn, and the protoplasmic movement anteriad alone continues.

b. What cells participate in the formation of the protoplasmic connections? If the possibility of the development of the abducens by the progressive differentiation of plasmodesmatous paths be excluded, the possibility remains that the abducens develops, either by the differentiation of a chain of cells, or as the product of protoplasmic movement of medullary neuroblasts. Dohrn ('90 a, '91) alone, of all of the students of the histogenesis of this nerve, has attempted to demonstrate the former mode of histogenesis. The fact, however, that later ('07) be admitted the inadequacy of the grounds upon which that opinion was based makes it unnecessary to call attention to the fallacy of his argument. Dohrn's premises were weak, not because he was a poor observer—no man has done more to enrich our knowledge of the histogenesis of nerves in selachians—but because his

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preparations were not suited to demonstrate the histogenesis of the neurofibrillae.

Filatoff ('07, p. 343) finds that the anlage of the abducens in reptile embryos appears primarily as a strand of mesenchymatous cells extending from the posterior rectus muscle towards the base of the medulla and as yet unconnected with the brain. The cellular strand is not fibrillar. How connection with the brain is effected, Filatoff is not able to state.

All other students of the histogenesis of the abducens agree that the cells of the abducens anlage have no genetic relation to it but are secondary and accessory. The fibers of the anlage arise as processes of medullary neuroblasts situated in the somatic motor column of the hindbrain, posterior to the otic vesicle. All have noted the greatly elongated nidulus, which, according to the writer ('98) extends through the first and second post-otic neuromeres (neuromeres VII and VIII). Belogolowy ('10 a, p. 270) makes the interesting discovery that in a 2.2 mm. embryo chick "the roots of the abducens extend through as many as five neuromeres." Later they arrange themselves into three groups, which however show no regular relation to the neuromeres. By a comparison of the relations of the abducens anlage to the neuromeres, Belogolowy concludes that the most anterior roots of the abducens of the chick take their origin from a neuromere next anterior to the one from which they originate in the dogfish (Squalus). Posteriorly the roots of the embryonic abducens in the chick are connected with those of the hypoglossus. The posterior roots of the abducens show a marked tendency to grow backwards as if to join those of the hypoglossus which lie immediately behind them. Still later some of the roots degenerate. Another important discovery made by Belogolowy is that of the existence of a transient somatic motor nerve, ventral to the ramus maxillaris trigemini and uniting peripherally with the oculomotor with which the abducens also unites. The inference of the medullary derivation of the neuraxons of the abducens is based on the evidence of the connection between deeply staining cells of the medulla and the fibers of the nerve anlage, from the time of the first appearance of the

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anlage (plate 8). The earliest stage represented (fig. 31) shows that the anlage, which already has two roots of origin, contains deeply staining fibers surrounded by an envelope of granular protoplasm. Mesenchymatous cells crowd thickly around the roots of the anlage so that it is impossible to distinguish their boundaries from the protoplasmic envelope. In this and later stages (figs. 32, 41, 37) the continuity of the processes of the medullary cells with the fibers of the anlage is unmistakable.

In later stages the number of roots increases to the number of five or six and there is a correlated increase in the number of medullary cells, the processes of which may be traced towards or into the roots of the anlage. In the meanwhile cells make their appearance in the nerve anlage (figs. 33, 36), but the comparison of closely connected stages indicates that these cells secondarily attach themselves to the anlage or, in advanced stages, migrate from the neural tube (fig. 39). None of them ever has the form or staining properties of neuroblastic cells, such as appear within the ganglionic nerves or within the wall of the medulla. Also, during the stages during which the fibers most rapidly increase in number these cells are distinctly peripheral in relation to the bundle of fibers. Furthermore, the fact that the fibers in successive stages grow centrifugally toward the myotome of somite 3, and that, in the earlier stages of growth, the number of fibers is greater in the proximal portion of the anlage than in the distal portion (figs. 42–44), accords with the supposition that the fibers have a medullary origin in central neuroblasts.

c. Have these protoplasmic connections a genetic relation to the neurofibrils? Students of the histogenesis of the abducens have paid little or no attention to the differentiation of the neurofibrils. There seems, however, little reason to doubt the genetic connection between the deeply stained fibers of the nerve anlage and the finer fibrils of the fully differentiated nerve. Their most important histogenetic change appears to consist in the splitting of the fibers into finer fibrils as the diameter of the fiber increases during growth. The granular envelope, so conspicuous in the anlage, gradually disappears and is replaced by

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the neurilemma cells as they penetrate among the fibers in advanced stages of histogenesis.

There appears to be no reason for doubting the identity of the fibers differentiated by the Vom Rath method with those which appear in Cajal and Bielschowsky-Paton preparations. They have practically identical appearance, form and relations, both in cross and longitudinal sections. So that if it be granted that the coarse fibrils seen in preparations made by the latter methods are genetically related to the neurofibrils of the adult nerve, the reasons apply with equal force to those which appear in Vom Rath preparations.

d. Is the individual neuraxon of the abducens anlage multicellular in origin or is it the process of a single cell? Reasons have already been stated why the abducens fibers may be regarded as products of protoplasmic movement and not of cell chains, and it seems unnecessary to repeat them. All the evidence favoring this conclusion for spinal somatic motor nerves and for the oculomotor and trochlearis may be advanced for the abducens. The proof is even more convincing in the case of the abducens, since development is simplified by the absence of connection with a ganglionated nerve.

e. By what means does the increase in length of the constituent neuraxons take place? This question may be answered in the same way as in the case of the other somatic motor nerves described, and has already been stated above. The evidence upon which the hypothesis of the plasmodesmatous origin of the nerve anlage is based is no less equivocal and unconvincing than that offered by its most recent exponent, Held ('09).

f. What is the source of origin of the cells of the abducens anlage? Since the abducens makes no connection with a ganglionic nerve and therefore receives no cells from that source, the cells of the anlage must either be derived from the mesenchyma or from the medulla or from both. Neal ('98) and Belogolowy ('10) were unconvinced of the medullary origin of the cells, which both derived from the mesenchyma. But Dohrn ('91) was undoubtedly correct in inferring the medullary origin of some of the abducens cells. The evidence of migration is quite as convinc-

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ing as that seen in spinal somatic motor nerves. A section through a root of the abducens is shown in figure 39 and the appearances are seen to resemble closely those of early stages of the development of ventral spinal roots. The evidence that mesenchymatous cells attach themselves to the anlage is equivocal but seems probable. Filatoff's ('07) observation of a migration of mesenchymatous cells from the anlage of the posterior rectus muscle is interpreted by the present writer as subsequent to the acquisition of connection between brain and myotome and as a part of the process of formation of the neurilemma. Filatoff advances no evidence that these cells have a genetic relation with the fibers of the definitive nerve.

g. What is the fate of the cells of the abducens anlage? As there is no sympathetic associated with the abducens in any vertebrate, the cells of the abducens can have only one fate if they persist in the adult nerve. In a non-ganglionic nerve they must form the neurilemma. With this conclusion all investigators, whatever their views regarding nerve histogenesis, agree.

h. What is the histogenesis of the neurilemma of the abducens? At the outset all of the cells of the abducens are peripheral in relation to the fiber bundle. Penetration of cells into this bundle is slow and has scarcely begun in a 25 mm. embryo. As in the case of the oculomotor and trochlearis, penetration begins in the region of the proximal roots, that is, in the oldest part of the nerve anlage. By the time the embryo has reached a length of 45 mm., however, cells have penetrated all parts of the fibrillar bundle and have begun to assume the characteristic form and relations of neurilemma cells.

i. To what an extent do the emigrated medullary elements go to form the sympathetic? The one essential respect in which the abducens differs from the other somatic motor nerves described is in the absence of the sympathetic in relation to the nerve anlage. As in the case of the hypoglossus, however, this feature appears correlated with the absence of connection with a ganglionic nerve, a correlation emphasized by Hoffmann ('00).

j. Summary of the histogenesis of the abducens. Like typical somatic motor nerves, the abducens acquires secondary connec-

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tion with the posterior rectus muscle by the continuous outflow of the protoplasm of cells in the somatic motor column of the hindbrain. Its fibers are directly connected with the medullary neuroblasts from which they arise, while its cellular elements are partly medullary and possibly, in part, mesenchymatous. From them develops the neurilemma of the differentiated nerve. No evidence that they are genetically related to the neurofibrils has been obtained. No sympathetic ganglion is associated with the abducens anlage or with the adult nerve.

5. What light does the study of histogenesis throw upon the question of the homology of pre-otic and post-otic metameres?

The demonstration of the similar histogenesis of the eye-muscle and spinal somatic motor nerves creates a strong presumption that pre-otic and post-otic divisions of the vertebrate body are fundamentally alike. It has been found that in no essential respect does the histogenesis of eye-muscle and spinal somatic motor nerves differ. The dorsal chiasma of the trochlearis and the lack of sympathetic connection with the abducens in no way invalidates the comparison. The hypoglossus nerve differs from the typical somatic motor nerves in precisely the same way as the abducens, but its comparability with spinal somatic motor nerves is unquestioned. In fact, if the relations of somatic motor and sensory nerves in Amphioxus and Petromyzon may be regarded as primitive, those of the abducens and of the hypoglossus are more primitive than those of other somatic motor nerves in Squalus. The absence of a sympathetic is likewise a primitive character. The study of the histogenesis of the eye-muscle nerves favors the prevalent conception of the vertebrate head as once like the trunk.

But the proof of the morphological similarity of segmental nerves depends, not on evidence of histogenetic similarity alone or central relations with the motor nidulus, but equally upon the peripheral distribution. So that the question arises whether or not the myotomes innervated by the eye-muscle nerves are serially homologous with those innervated by spinal somatic motor nerves.

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The study of histogenesis has shown that connection between muscle and nerve is not primary but secondary. This suggests the possibility that new segmental relations may be acquired by somatic motor nerves and that a nerve may invade territory foreign to it. In this way some peculiarities in the relations of eye-muscle nerves may be explained.

RELATIONSHIPS OF THE EYE MUSCLE NERVES

1. Is the musculature innervated by the eye-muscle nerves somitic musculature?

The eye-muscle nerves innervate muscles derived from Van Wijhe's first, second and third somites. The oculomotor innervates muscles differentiated from the first, the trochlear innervates that derived from the second, and the abducens is connected with a muscle formed from the third and a part of the second (Dohrn '07). Are these muscles serially homologous with those innervated by spinal somatic motor nerves? This obviously depends upon the somitic nature of Van Wijhe's three 'somites.'

They have been regarded as true somites by many morphologists including Van Wijhe ('82), Oppel ('90), Miss Platt ('91, '97), Hoffmann ('94), Neal ('96, '98), Fürbringer ('97), Koltzoff ('01), Killian ('91), Boecke ('04), Filatoff ('07) and their presence has been demonstrated in such diverse groups as Selachii (Van Wijhe '82, Miss Platt '91, Hoffmann '94, Neal '96, Braus '99, Johnston '09); Cyclostomes (Koltzoff '01); Teleosts (Boecke '04); Amphibia (Miss Platt '97); and Reptiles (Oppel '90, Filatoff '07).

On the other hand the eye muscles have been regarded as splanchnic muscles by Stannius ('51), Langerhans ('73), Balfour ('78), Marshall ('81, '82), Dohrn ('85, '87, '04, '07), Houssay ('90), Hatschek ('92), Rex ('97, '05) and Sewertzoff ('98), and the presence of true somites in the pre-otic region has been denied by Kastschenko ('88), Rabl ('92) and McMurrich ('12). Sewertzoff ('98 b) bases his objection to the inclusion of the second myotome in the series of somitic muscles upon the con-

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clusion of Froriep and Miss Platt that the trochlearis is a mixed (splanchnic motor) nerve, and not upon the basis of direct evidence.

Dohrn ('04) concluded that the superior oblique muscle is splanchnic and not somitic on the evidence that a portion of the splanchnic (ventral) mesoderm of the mandibular cavity shifts during development to a dorsal position as a result of the cephalic flexure of the brain. From this displaced mesoderm, according to Dohrn arises the masseter muscle, the superior oblique muscle and a portion of the posterior rectus muscle.

Filatoff ('07, p. 354) takes exception to this inference of Dohrn on the ground that it is difficult to distinguish dorsal from ventral mesoderm in the mandibular cavity and more especially to determine what is dorsal and what is ventral during the process of shifting relations in successive stages. Filatoff finds that the superior oblique muscle in Emys arises from the dorsal segmented portion of the mandibular cavity.

Against the somitic value of the pre-otic mesodermic segments it has been argued that the head of the vertebrate ancestor was, like that of Tunicate larvae, unsegmented; that the supposed segmentation is not actually metameric but is the result of mechanical influence of other organ systems; that the mesodermic divisions are irregular in size and inconstant in number; that they are discontinuous with those of the trunk; that they do not differentiate sclerotome and myotome, at least in the typical manner; that the topographic relations to nerves are different from those of trunk somites. But, since renewed investigation has disproved many of these assertions, the argument in favor of the somitic value of Van Wijhe's somites seems on the basis of the following evidence, much the stronger of the two alternatives.

That Van Wijhe's somites are serially homologous with those of the trunk seems sufficiently established by the repeated confirmation of their presence in diverse groups of vertebrates; and on the ground that their segmentation is independent of the visceral segmentation; that Van Wijhe's somites form a continuous series with those in the trunk; that they are dorsal in relation to chorda and dorsal aorta; that their development is

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progressive, beginning with the neck region; that they differentiate into myotome and sclerotome; that their muscles are primarily differentiated from the median wall; and that they correspond numerically, as in the trunk region, with the neuromeric divisions of the neural tube. They, therefore, constitute the best established evidence of the primitive metamerism of the vertebrate head and of its comparability with the trunk. The somitic nature of the muscles derived from them seems therefore, indisputable.

2. Are the relations of the oculomotorius comparable with those of a somatic motor spinal nerve?

a. How is the relation of the oculomotor to the ramus profundus to be interpreted? The oculomotor nerve resembles a somatic motor nerve not only in its histogenesis but also in its central and peripheral relations.

Like a spinal somatic motor nerve, it arises from a nidulus in the somatic motor column of a neuromeric segment of the neural tube and innervates muscles derived from a somite serially homologous with those of the trunk. Furthermore it becomes connected with a ganglionic nerve after the manner of typical spinal somatic motor nerves.

This connection with the ramus profundus V, however, needs closer scrutiny. True, it is a ganglionic nerve, but is it certain that all ganglionic nerves are morphologically comparable? Our present knowledge of nerve components and their differences in the various cranial nerves, as demonstrated by the investigations of Strong ('95), Herrick ('99) and Johnston ('05 a), discourages the indiscriminate comparison of nerves on such superficial grounds as the possession of a ganglion. Therefore one, who maintains the similarity of the relations of the oculomotor with spinal somatic motor nerves, is bound to demonstrate the morphological similarity of the ramus ophthalmicus profundus V with spinal somatic sensory nerves. That they are similar seems proved first by their similar histogenesis from neural crest cells; second, by their similar peripheral distribution as general cuta-

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neous nerves; and third by their common classification as somatic afferent nerves.

Three objections, however, may be raised against this homology; first, that while spinal somatic sensory nerves grow median to the myotome, the ophthalmicus profundus, like other typical cranial nerves, grows lateral to the somites; second, that cellular elements enter the ganglion of the ophthalmicus profundus from the skin, while the cellular elements of spinal sensory nerves are exclusively derived from the neural crest; and third, that the profundus is not an independent segmental nerve but a sensory branch of another nerve.

The first of these objections may be met by calling attention to the fact that in some cases, for example in the post-otic region of Ammocoetes, typical cranial nerves lie partly lateral and partly median to the myotomes, indicating that no sharp line of demarkation can be drawn on this basis between cranial and spinal somatic sensory nerves. Such differences appear to be correlated with differences in the relative size of the somite. Furthermore, there are comparative anatomical grounds for thinking that somatic sensory nerves were primarily inter-myotomic in position. From such primitive relations the present modified relations of cranial and spinal somatic sensory nerves may readily have been derived.

The second objection is more serious, but if the comparability of the somatic sensory nerves of Amphioxus and Squalus be granted, it will be seen that the cranial somatic sensory nerves have retained the primitive relations of the former, while the absence of direct contact with the skin in the case of spinal somatic sensory nerve ganglia, may be regarded as a secondary modification. In this respect, as in respect to the retention of a mixed function, typical cranial nerves appear more conservative than spinal nerves. Therefore, while it must be admitted that the cranial somatic sensory ganglia are more complex in their derivation than are spinal ganglia and that the serial homology of the two is incomplete, nevertheless their partial homology appears demonstrable.

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Finally, the fact the fibers of the ophthalmicus profundus enter the medulla in common with those of the trigeminus will not seem to morphologists a serious objection to the comparison of the profundus with spinal somatic sensory nerves, since it would seem a matter of indifference whether somatic sensory fibers enter the brain by one path or another. In the case of the union of the roots of once independent ganglia we seem to have to do with a particular case under the general principle of the centralization of function in the region of the medulla. Analogous instances may be found in all organ systems.

Taking all the facts into consideration there appears to be no insuperable objection to the view that the ophthalmicus profundus is serially homologous with spinal somatic sensory nerves.

b. How is the relation of the oculomotorius to the ciliary ganglion to be interpreted? The comparison of the profundus nerve with spinal somatic sensory nerves is still further strengthened by the evidence of the relations with the ciliary ganglion which have been found above to be those of a somatic motor nerve to a sympathetic ganglion. The facts which prove the sympathetic character of the ciliary anlage have already been stated above and need no restatement. The ciliary ganglion of Squalus is to be regarded as partly, if not exclusively, a sympathetic ganglion. So that in its relations with a sympathetic ganglion the oculomotor forms no exception in the series of morphologically similar somatic motor nerves.

c. How may the relation of the oculomotorius to four eye muscles be best interpreted? The distribution of the oculomotor to four muscles may appear to require interpretation. The fact, however, that all of these muscles are derived from a single myotome by a process of splitting and that this splitting is correlated with the considerable enlargement of the eye-ball; furthermore, that the innervation of more than one muscle by a single somatic motor nerve is by no means exceptional, brings these relations also into line with those of spinal somatic motor nerves. The oculomotor, therefore, in its histogenesis and in its relations to a somatic sensory ganglion, to a sympathetic ganglion and to

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somatic musculature may be considered serially homologous with spinal somatic motor nerves.

d. Conclusions regarding the morphology of the oculomotor. It is scarcely necessary to say that the conclusion that the oculomotor is serially homologous with spinal somatic motor nerves has not been reached by all morphologists. It is, however, the opinion of the majority, including Van Wijhe ('82), Beard ('85), Hoffmann ('86–'00), His ('88), Martin ('90), Dohrn ('90, '91), Zimmermann ('91), Kölliker ('96), Neal ('96, '98), Koltzoff ('01), Carpenter ('06), Filatoff ('07), Belogolowy ('08) and also, on the basis of anatomical evidence, Muck ('15), Bell ('30), Stannius ('49), Bonsdorff ('52), Budge ('55), Huxley ('74, '75), Schneider ('79), Gaskell ('86, '89), Strong ('90), Fürbringer ('97), Wiedersheim ('98), Gaupp ('99).

On the other hand, it has been regarded as a splanchnic motor nerve homologous with the trigeminal by Balfour ('78), Marshall ('81, '82), Dohrn ('85, '87), Houssay ('90), Hatschek ('92), Sewertzoff ('98), and as a somatic sensory or mixed nerve with coenogenetic atrophy of the sensory element by Marshall ('82), Rabl ('89), Martin ('90), Miss Platt ('91), Mitrophanow ('92, '93), Sedgwick ('94), Sewertzoff ? ('99), Gast ('09), and on anatomical grounds by Schwalbe ('79, '81) and Gaskell ('89.)

The most recent argument in favor of the latter opinion is that given by Gast. He admits that in its first anlage, the oculomotor develops in the same way as the anlage of a somatic motor nerve. On page 420 he states that naked neuroblast processes grow from the neural tube, unite to form a naked fiber bundle, grow to a segmental ganglion, and receive their sheath cells from it. Medullary neuroblasts also migrate into the nerve anlage. Sheath and sympathetic cells wander from the mesocephalic ganglion into the nerve anlage but retain connection with their source by a ramus communicans, a phenomenon quite in line with that of typical somatic motor nerves.

On the other hand, he says, there are indications that lateral horn elements are combined with these ventral root elements. In the first place, the close relations with the mesocephalic ganglion through which the oculomotor fibers grow in some instances

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confirm this view. In other cases the oculomotor assumes very close relations with the ganglionic placode connected with the mesocephalic ganglion. Again, there is evidence of the anlagen of sensory nerves in connection with the oculomotor. The proof of this (p. 401) consists in the fact that a short cell-chain, free from fibers, extends from the mesocephalic ganglion toward the oculomotor anlage. The absence of a fiber in the cell-chain appears to Gast to exclude the possibility that the cells are in the process of migration centrad along a motor fiber of the oculomotor. On the other hand, Gast (p. 402) regards the evidence given by Mitrophanow ('93) and Sedgwick ('92) in favor of the mixed function of the oculomotor as fallacious. But Miss Platt ('91) may have seen what he regards as evidence of sensory elements in the oculomotor.

While Gast admits that this conclusion appears to conflict with the evidence of the position of the nidulus of the oculomotor, he asks if it is not conceivable that Dohrn's suggestion is correct—that the lateral and ventral niduli have united together. Then there is the possibility that the separation of ventral and lateral niduli in the head region is a coenogenetic separation and that they were primitively united. Gast, however, is of the opinion that the union of lateral and ventral niduli assumed for the oculomotor is a secondary one, as Dohrn suggested.

On the basis of this supposition, Gast (p. 421) indulges in the following speculation:

> The segmentally arranged mesocephalic-oculomotorius system with its sensory and motor roots becomes secondarily separated into sensory and motor elements, whereby the motor neurones of the oculomotor retain their central connections, while the sensory neurones of the mesocephalic ganglion acquire a new root. In the case of the Selachii this root formation came to pass in such a way that a commissure was formed between the individual ganglia of the anterior head region (trigeminal, trochlear, mesocephalic and the ganglia anterior to these). This commissural nerve gradually assumed the character of a root, while fibers of the segmental sensory roots proportionally degenerated. To-day, indications of these primary sensory roots are found in the oculomotor as well as in the trochlear.

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The foundation for Gast's speculation consists, primarily, in the evidence of close or intimate relations with a cerebro-spinal ganglion. But if such logic were rigidly followed, it would be necessary to regard every spinal somatic motor nerve as a lateral-horn (splanchnic motor) nerve, since close and intimate relations with a cerebro-spinal ganglion is characteristic of spinal somatic motor nerves in Squalus.

The supposed demonstration of the participation of sensory elements in the genesis of the oculomotor is one that would satisfy only on the basis of a strong presumption in its favor. The position of the nidulus of the oculomotor and its peripheral distribution create a strong presumption against the assumption. Spindle-shaped cells lying in the mesenchyma between the profundus ganglion and the oculomotor nerve are not necessarily neuroblasts. Spindle-shaped cells may be found almost anywhere in the mesenchyma. Even if it be admitted that the evidence that these cells are in the process of migration toward the oculomotor anlage is convincing, Gast does not know their fate. They may form neurilemma or they may enter the sympathetic or what-not. Their later histogenesis is wholly unknown. Gast has not used neurofibrillar stains in order to ascertain their neuroblastic character. It would be surprising if morphologists accepted Gast's conclusion upon the basis of the slight evidence he is able to present in its favor.

The evidence in favor of the view that the oculomotor nerve is a mixed nerve homologous with typical cranial nerves such as the trigeminal is so unconvincing, while the evidence of its histogenesis and its central and peripheral relations so strongly support the supposition that it is a somatic motor nerve, as the majority of morphologists have believed, that the acceptance of the latter seems unavoidable. This view at least does not require support from such an unproved assumption as the secondary fusion of lateral and ventral motor niduli.

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3. Are the relations of the trochlearis comparable with those of a somatic motor spinal nerve?

There is practically a consensus of opinion that in its most essential relations, namely, in its relation to a nidulus in the somatic motor column of the hindbrain, the relations of the trochlear are comparable with those of spinal somatic motor nerves. There is less general agreement, and yet a considerable majority of morphologists agree, that the trochlear innervates somitic musculature. The main objection which has been advanced against this conclusion has been that raised by Stannius ('51) and Langerhans ('73) of the different histological structure of the superior oblique muscle, which, according to these investigators, resembles splanchnic rather than somitic musculature. This objection may be met by denying the truth of the assertion as a generalization for all vertebrates. Differences in size and in detail between fibers of the eye muscles and those of the lateral trunk muscles may exist—especially in those forms in which the eye muscles are differentiated from a loose mesenchyma, but in forms like Squalus, there is no important histological difference between the muscles of the eye and those of the trunk. Such slight differences as do obtain may be ascribed to differences in environment. That they are not due to difference in genesis appears demonstrated by the evidence of the somitic origin of the eye muscles. Therefore, in histological structure as well as in its histogenesis and in relations, both central and peripheral, the trochlearis conforms to the type of spinal somatic motor nerves. But there are other relations of the trochlear that may profoundly affect our views of its morphology.

a. How may the 'ganglion' of the trochlear be interpreted? Gast ('09) thinks that the trochlear 'ganglia' described by Dohrn ('85), Hoffman ('89), Martin ('90) and Froriep ('91), afford very clear proof that the trochlear is a 'complete segmental nerve.' Dohrn ('07, p. 396) regarded the evidence that in Torpedo embryos rudimentary centripetal ganglionic nerve fibers unite with the trochlearis as supporting the view that the trochlear is a lateral-horn nerve. I ('98) had interpreted the same evidence

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as proof of the derivation of the neurilemma from the neural crest. Dohrn, however, thinks that the evidence of cellular migration into the trochlear anlage from the ramus superficialis indicates that genetic relations between the trochlear anlage and rudiments of ganglia still persist today, even though they are merely transient.

Dohrn's thorough investigation of the histogenesis of the trochlear in elasmobranchs, however, indicate that the so-called ganglia of the trochlear are irregular fragments of the neural crest lying in the region through which the trochlear grows; further, that the trochlear anlage in such forms as Pristiurus attains connection with the myotome without any relation whatever with these fragments, which develop in inverse ratio with the development of the ramus superficialis V, of which therefore they appear to be the equivalent. In other words, the relations of the trochlear with these 'ganglia' of the Torpedinidae in which they appear seem similar to its relations with the ramus superficialis V in the Squalidae. This equivalency is recognized by Gast ('09) who says that the sensory elements of the trochlear which appear as ganglia in the Torpedinidae are represented by the ramus ophthalmicus superficialis V in the Squalidae.

Whether or not this equivalency be admitted, the relations of the trochlear to the 'ganglia' of the nerve resemble those of a spinal somatic motor nerve to the ganglionic or nervous derivatives of the neural crest. Such relations disprove the somatic motor character of the nerve in question quite as little in one case as in the other.

While in Squalus the trochlear anlage has no such relations to irregular fragments of the neural crest as in the Torpedinidae, the nerve does have relations to cell masses which precisely resemble those of the oculomotor to the anlage of the ciliary ganglion, or those of a spinal somatic motor nerve to sympathetic anlagen. Such relations of the trochlear anlage are represented in figures 54 and 55. With a strong presumption in favor of the view that the trochlear is a somatic motor nerve as evidenced by its histogenesis and by its central and peripheral connections the most reasonable interpretation of the mass of cells

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at the place of union of the anlagen of the superficialis and the trochlear is that it is sympathetic. Like the cells of all sympathetic ganglia those of the trochlearis appear to come from a sensory ganglion. In both instances they collect in the region where sensory and motor fibers unite. Against this view may be urged the fact that there is no sympathetic in relation to the adult trochlear nerve. But the objection loses much of its force when it is remembered that transient sympathetic ganglia are not uncommonly found in the trunk region of elasmobranchs.

This supposed sympathetic ganglion of the trochlear anlage must not be confused with those fragments of the neural crest which Dohrn ('85) and others have called ganglia of the trochlearis. Such 'ganglia' appear, as suggested by Dohrn ('07) and Gast ('09), to be comparable with degenerated portions of the superficial nerve and not with sympathetic ganglia. Belogolowy ('10 b) finds in reptile embryos a ganglion present at the point of anastomosis of the trochlearis anlage with the ramus ophthalmicus superficialis trigemini. Belogolowy expresses the opinion (p. 70) that the so-called ganglia of the trochlearis are really the ramus ophthalmicus superficialis trigemini which is represented in some forms by scattered clumps of cells. With this opinion the writer is in full accord.

b. How may the innervation of a muscle derived from a somite (Van Wijhe's second) also innervated by the abducens be interpreted? Another problem presented by the relations of the trochlear is the fact that it innervates a muscle derived from a somite also supplied by the abducens nerve. This comes about in the following manner: A portion of the myotome of Van Wijhe's second somite unites with the myotome of the third somite to form the posterior rectus muscle. Miss Platt ('91), with characteristic accuracy, observed this connection, but was led to infer its later degeneration and to confirm the conclusion of Van Wijhe ('82) that the posterior rectus muscle is derived exclusively from the third somite. Lamb ('02) reached the same conclusion. But Dohrn ('07), after a careful reinvestigation of the development of the superior oblique muscle, asserted the

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persistence of that portion of the second myotome in connection with the myotome of the third somite. Dohrn has affirmed its persistence correctly. There is no doubt whatever that it persists in the superior oblique muscle of Squalus. Its relations are diagrammatically shown in figure 81. Thus it comes about that the trochlear and abducens nerves innervate portions of the same somite. In this way a problem in nerve relations is presented which will be fully discussed in connection with the problem of the relations of the abducens nerve. Suffice it to say here that this relationship of two somatic motor nerves to a single somite does not in any way affect adversely our views of their real morphology. As a matter of fact, emphasized by Bardeen ('04), all typical somatic motor nerves have a bimeric distribution to two adjacent myotomes. The most perplexing problem raised in this connection is that there is reason to think that the trochlear and abducens nerves do not belong to successive metameres. This question will be taken up later. But, even more difficult for one who attempts to demonstrate the somatic motor character of the trochlear, is the problem of its dorsal chiasma. In this feature the trochlear is the most peculiar nerve in the vertebrate body.

c. How may the dorsal chiasma of the trochlear be best explained? Van Wijhe ('86), in order to explain the dorsal emergence of the fibers of the trochlearis, assumed that, as a result of the extension of the anterior column to the olivary body and to the loop extending behind the corpus quadrigeminum, the root of the trochlear was drawn over the loop into its present position.

According to His ('88) the peculiar relations of the trochlear may possibly be explained as the result of the flexure of the neural tube in the region of the isthmus, a condition which he thinks is favorable to the sagittal growth of the neuraxon processes of the neuroblasts at the base of the cerebellum.

Rabl ('89), however, on the basis of observations on the selachii, birds and mammals, concluded that the roots of origin, both of the oculomotor and of the trochlear were primitively dorsal, but that gradually, through the enlargement of the peduncular paths, the root of the oculomotor was shifted to the ven-

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tral surface of the brain, while the trochlear has retained its primitive position. It may readily be seen, however, that such considerations have to do with the dorsal emergence of the trochlear fibers rather than with the chiasma of the nerve.

Martin's ('90) unconfirmed and incredible assertions regarding the transmigration of the trochlear nidulus appear to deserve no restatement, although they were accepted tentatively by both Minot ('92) and Kölliker ('96) so far as they relate to a central origin of the trochlear chiasma. Kölliker, however, finds it difficult to conceive of a transmigration of a nidulus, although von Lenhossek and Ramón y Cajal have inferred a migration of neuroblasts from the ventral column of the tube into the sensory roots. An extensive migration of neuroblasts therefore appears possible.

Fürbringer ('02, pp. 134–136) has given the most thorough consideration to the problem of the chiasma of the trochlear and his hypothesis, although affected by his views of the primary and unalterable connection of nerve and muscle, seems to be the most elaborate of all that have been advanced. Following an idea advanced earlier by Hoffmann ('89), Fürbringer suggests that the trochlearis may have innervated musculature belonging to the parietal eye. According to Fürbringer the parietal eye (or pair of eyes) was situated primarily near the paired lateral eyes, which were then slightly differentiated and probably occupied a more dorsal position than later. The aberrant musculature connected with both kinds of eyes may have very early separated itself—as the course of the nerve indicates—from the dorsal portions of the neighboring myotomes and may, in correlation with the primitive condition of the eyes, have been in a very slightly differentiated and—so to speak—fluid condition, with its fibers extending in various directions. Those portions of the muscle which extended somewhat diagonally or transversely had the tendency, like other muscles extending toward the median line of the body, to migrate over into antimeric territory. There was nothing like a median fin in the region to hinder this migration, which could occur freely.

With the degeneration of the parietal eye the musculature which became associated with it disappeared. The muscles of

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the lateral eyes, however, which at that time were in close proximity to one another did not degenerate but became attached to, and at the same time migrated with newly differentiated fibers, to the eye of the opposite side where they increased in size while the original muscles of that side atrophied. In this way they formed the present superior oblique muscle, the nerve of which with its dorsal chiasma—primarily peripheral—still discloses the early history of the transmigration of its muscle. Then with the higher development of the retina of the lateral eyes there came an enlargement of the centers within the brain, especially a greater development of the roof of the midbrain, which extended backward over the place of emergence of the trochlear fibers and covered it, so that a part of its root as well as its chiasma was shoved backward and at the same time enclosed within the wall of the brain. The lateral eyes were not restricted to that dorsal muscle derived from the second myomere of the opposite side but very soon acquired connections with more ventral musculature innervated by the oculomotor and abducens, and, as the eyes moved into a ventral position, the muscles became enlarged and differentiated.

In support of this hypothesis, Fürbringer advances the following considerations: First, in defense of the assumption that the parietal eye once possessed a musculature of which today there is no evidence (with possibly the exception of the unconfirmed case in mammals mentioned by Nicholas ('00) who claimed to demonstrate rudimentary striated muscles in the pineal region of the ox), he argues that the absence of parietal muscles today by no means proves that they never existed. Many skeletal structures have existed in fossil species without leaving a trace in modern vertebrates. Typhlichthys has no eye muscles but its ancestors must have had them. The assumption of an antimeric transmigration of the hypothetical ancestral eye muscles has met both opposition (Dohrn '01) and support (Gaskell '01). In reply to the opposition, Fürbringer cites many cases of the extensive migration of muscles in all directions within the vertebrate body. Many instances of the transmigration of musculature on the ventral side of the body are known, as for example the muscles innervated by the facialis, vagus and hypoglossus,

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as well as some parts of the M. sternalis. Since there is no median fin in the head region to prevent transmigration, it may have occurred there as readily as in the ventral trunk and head region.

The vagrant nature of the superior oblique muscle is evinced by the considerable variation in the origin and insertion of the muscle as well as in its extended migration in the embryo.

Several fairly obvious objections may be raised against Fürbringer's ingenious hypothesis: First, the absence of any direct evidence from comparative anatomy and embryology that any vertebrate muscle has migrated in toto from one side of the body to the other; Second, the complete failure of ontogenesis to support the hypothesis. Ontogenesis is hardly so discredited, even by Fürbringer, that this lack of ontogenetic support can be wholly ignored; Third, the total lack of evidence of an epiphysial musculature. Nicholas ('00) did not demonstrate the actual connection of rudimentary muscles with the epiphysis; Fourth, the improbability of such a swapping of muscles as is assumed in the hypothesis. Why the lateral eyes should lose muscles which they already possessed and adopt those of another degenerating organ is not perfectly obvious. Still other objections might be mentioned but it seems unnecessary to multiply them.

Of course it may be said that no hypothesis dealing with phylogenetic changes so remote as the origin of the trochlear chiasma may be advanced which will seem so compelling as to preclude criticism. To many, Fürbringer's hypothesis will appear a reasonable one, on the assumption that nerve and muscle are phylogenetically inseparable. The relations of the trochlear and superior oblique muscle have always seemed a stumbling block to the supporters of that assumption, the truth of which does not seem more certain as the result of the difficulty of explaining the chiasma of the trochlear.

Fewer difficulties, it might appear, would meet an hypothesis which assumed the secondary connection of nerve and muscle by means of the free outgrowth of the nerve fibers.

Johnston ('05, p. 210) suggests that:

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The course of the root fibers dorsally through the brain wall may be due to the course of the fiber tracts through which they run. The position of the nucleus of the nerve relative to the tracts which form the ansulate commissure in typical fishes suggests strongly that the axones from the cells of the trochlearis nucleus may have followed some of these bundles as the path of least resistance. The tracts between the tectum opticum and the base of the oblongata, the tracts between the inferior lobes and the cerebellum, and others, all running more or less dorso-ventrally in the side wall of the brain and decussating ventrally at the level of the trochlearis nucleus—these bundles, which lie ectal to the nucleus of the trochlearis, may have constituted an effective barrier to the axones of the trochlearis in their attempt to reach the ventro-lateral surface of the brain. The axones may then have turned upward along the ental surface of these bundles until they reached the dorsal surface of the brain. If the fibers were thus directed in their course they would be carried to the mid-dorsal line before gaining an exit from the brain and if they then grew straight on they would pass to the opposite side.

Filatoff ('07, pp. 366–7)thinks that certain phenomena in the development of the brain may help to explain the peculiar origin of the trochlearis. At the time of the formation of the cephalic flexure the roof of the midbrain, which up to that time formed a part of the thin upper wall, thickened. The production of this thickening may be explained in the following way. By the development of the flexure the cells of the floor of the midbrain become most strongly compressed, since they come to lie directly in the place of flexure, and they seek to elongate themselves in the most direct way where the pressure is a little less strong, namely towards the upper wall. The point at which the trochlearis arises is directly determined by this elongation of the cells. The point of emergence of the trochlearis fibers is shoved from the ventral to the dorsal side.

Figure 82 of this paper suggests two possible phylogenetic stages in the development of the trochlear chiasma. An earlier stage is represented on the left of the diagram and a later stage, corresponding essentially to that seen in some elasmobranch embryos, is shown on the right. It is assumed that originally the trochlear, as a somatic motor nerve, was distributed to the myotome of the second somite of its own side after the fashion of typical somatic motor nerves, and that this myotome, when

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fully developed, extended dorsally to form a union or interdigitation with the antimeric myotome. As Fürbringer has correctly stated, no skeletal structures would prevent the extension of fibers across the median plane. It may be imagined that this extension of muscle fibers across the median plane was correlated with the muscular development of the prostomial region. Petromyzon still shows (fig. 77) the extension of myotomes into this region. Under such conditions slight variations in the length of the nerve fibers which grow to connect with these muscles might bring about a peripheral chiasma. The possibility that such muscles had connections with the epiphysis is not excluded, but such a supposition does not seem necessary. Changes in the extension and direction of growth of muscle and nerve fibers in this region may have been correlated with the development of the cephalic flexure which would seem to require some adjustment of the muscles since the forebrain and midbrain regions were flexed into a more ventral position. The final result of the flexure, however, appears to have been a shifting of those portions of the musculature which persisted in this region into a more ventral position and a separation of the muscles which had been apposed in the median plane above the brain wall.

The growth and great enlargement of the lateral eyes also brought about changes in the (Van Wijhe's) second myotome, which became split into dorsal and ventral moities (*my. 2 v.l.*, *my. 2 m.*, *my. 2 d.l.*) in precisely the same way as occurs ontogenetically in the post-otic muscles of Petromyzon as a result of the growth of the otic vesicle (figs. 78, 79).

It may be assumed that, as in the latter case, the median portion of the myotome degenerated, together with its branch of the somatic motor root (trochlear nerve), while the lateral moiety became innervated by a branch of the abducens (fig. 82, *abd.*). The dorsal moiety, however, retained its connection with the trochlear nerve, and possibly also with fibers from both sides of the brain, by means of a dorsal, peripheral chiasma. Then, when later this dorsal moiety degenerated with the exception of that portion which became attached to the eye-ball to form the external oblique muscle (crossed hatched in the dia-

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gram) the result would be essentially the conditions that obtain today in those forms of selachian embryos in which a peripheral chiasma persists (fig. B, p. 25), and are shown in the right hand side of the diagram. It is necessary, however, to assume that phylogenetically the chiasma came to be more and more central and that gradually the fibers of the trochlear nerve became exclusively crossed fibers. What factors determine the survival of the crossed fibers and the elimination of the direct is no less mysterious than those which have produced the ventral chiasmae of the eye and the pons. Possibly purely mechanical conditions of the sort suggested by the writer ('98) and by Johnston ('05) are responsible. All who have discussed the chiasma agree in one essential point—namely, that the chiasma of the trochlear is secondary and that it constitutes a coenogenetic modification of a somatic motor nerve. Therefore, its existence does not affect our views of its morphology. All other questions are subordinate to this, and it does not appear greatly to matter whether or not the true history of the origin of the chiasma has been or ever will be told.

d. Conclusions regarding the morphology of the trochlearis. The trochlear has been regarded as a somatic motor nerve on the basis of anatomical evidence by Stannius ('49), Huxley ('74, '75), Schneider ('79), Gaskell ('86, '89), Osborn ('88), Strong ('90), Fürbringer ('97), Wiedersheim ('98), and Gaupp ('99) and on the basis of embryological evidence by Van Wijhe ('82), His ('88), Martin ('90), Dohrn ('90, '91), Zimmermann ('91), Hoffmann ('94), von Kölliker ('96), Neal ('96, '98, '12), Koltzoff ('01), Filatoff ('07), Belogolowy ('08, '10).

On the other hand it has been regarded as a splanchnic motor nerve on the basis of anatomical evidence by Bell ('30), Hatschek ('92), Haller ('98), Fürbringer ('02). Stannius ('51) and Langerhans ('73) reached the same conclusion on the basis of the histological structure of the superior oblique muscle; while Balfour ('78), Marshall ('81, '82), Dohrn ('85, '90, '04, '07), Béraneck ('87), Houssay ('90), Hatschek ('92), von Kupffer ('94) and Sewertzoff ('98) supported this view on the basis of ontogenetic evidence.

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Then too we have the view that the trochlear was primitively a dorsal nerve, innervating visceral musculature, advanced by Schwalbe ('79, '81), Dohrn ('85) and von Kupffer ('95); innervating somitic musculature, by Miss Platt ('91) and Hoffmann ('97, '99, '00); and finally that it was primarily purely sensory and possibly secondarily mixed but eventually losing its sensory components, by Rabl ('89, possibly), Martin ('90), Oppel ('90), Froriep ('91), Platt ('91), Mitrophanow ('92, '93), von Kupffer ('95), Hoffmann ('89, '97, '99, '00), and Sewertzoff ('98).

This brief summary of the views held regarding the morphology of the trochlearis will possibly suffice to show that opinion is about equally divided for and against the view that the trochlear is a somatic motor nerve. Since a detailed statement of the arguments, for and against, has been given by both Fürbringer ('02) and Dohrn ('07) it appears to be unnecessary to discuss slightly divergent individual opinions.

The chief argument in favor of the comparability of the trochlear with dorsal ganglionic nerves appears to be, not the evidence of its dorsal origin, since the point of emergence of its fibers is ultra-dorsal rather than dorsal and in this respect it differs as much from a dorsal nerve as from a ventral one, but the evidence of its relations with neural crest cells, either aggregated as the ramus superficialis V, or as scattered clumps of neural crest cells called ganglia by several investigators. Dohrn ('07) is right in asserting in contradiction to Neal ('98) that the relations of the trochlearis with the ramus superficialis or with transient clumps of neural crest cells have a phylogenetic significance. But the fallacy of regarding the trochlear as a dorsal nerve on the basis of such evidence has already been pointed out above. By a similar argument every somatic motor nerve of the body which becomes associated with a ganglionic nerve must be regarded as a dorsal nerve.

Dohrn is also correct in asserting that the evidence of the formation of the trochlear as a bundle of neuraxon processes of medullary neuroblasts proves that the nerve is a somatic motor nerve no more and no less than it proves the trochlear to be a

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splanchnic motor nerve. It is not a little surprising, however, that Dohrn seems to have forgotten that the motor nidulus of the trochlear has the relations of a somatic motor nerve and not those of a splanchnic motor nerve. In the heat of the attempt to prove the trochlear a dorsal nerve Dohrn seems also to have forgotten that somatic motor nerves have relations with ganglia, both dorsal and sympathetic, comparable with those of the trochlear. Of his special views regarding the segmental relations of the trochlear consideration will be given later.

On the other hand it has been shown that in every essential detail of central and peripheral relationship, of histogenesis and of adult histological structure the trochlear must be regarded as a somatic motor nerve. Its peculiarity consists in one special feature—its chiasma, but in this respect it differs quite as much from a typical dorsal nerve as from a ventral somatic motor one. The interpretation of the mode of genesis of this chiasma is quite as easy upon the assumption that it is morphologically a somatic motor nerve as upon the assumption that it is a dorsal nerve, the opinion of Dohrn ('07) to the contrary notwithstanding.[1]

4. Are the relations of the abducens comparable with those of a somatic motor spinal nerve?

As a purely motor nerve, with a ventro-lateral nidulus and with a distribution to somatic musculature, there seems to be no good reason for questioning the serial homology of the abducens with spinal somatic motor nerves. The absence of a sympathetic ganglion is one striking point of difference, however, which is correlated with the absence of any connection with a dorsal nerve. In both these respects the abducens resembles the more primitive somatic motor nerves of Amphioxus and Petromyzon, and the absence of a sympathetic ganglion is to be regarded as a case of the retention of an ancestral character.

[1] Dohrn ('07, p. 410) thinks that the writer's view of the trochlear as a somatic motor nerve makes the solution of the problem of the chiasma more difficult.

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The second and more important point of difference between the abducens and spinal somatic motor nerves is its distribution as a post-otic nerve to pre-otic myotomes. Instead of innervating musculature of its own metamere, it is distributed to myotomes of anterior metameres (fig. 76). This relation, therefore, demands interpretation.

a. How may the innervation of pre-otic musculature, the posterior rectus muscle, by a post-otic nerve, the abducens, be interpreted? Are the myotomes innervated by the eye-muscle nerves post-otic myotomes which have migrated into pre-otic territory? In the attempt to solve the problem presented by the distribution of the abducens, namely, the problem of the distribution of a post-otic nerve with a post-otic nidulus to pre-otic muscle, two alternative hypotheses suggest themselves.

According to the first hypothesis, the posterior rectus muscle is to be regarded as a post-otic muscle which has migrated in the course of phylogeny into pre-otic territory, carrying with it the associated nerve, the abducens. As would be expected the nidulus of the abducens has retained its primitive position in the medulla, posterior to the otic capsule. One of the conditions which has brought about the migration of the posterior rectus muscle may have been the reduction and final disappearance of the pre-otic muscles, through the development and hypertrophy of the sense organs, cranial ganglia and cartilage cranium. Then, after the atrophy of the pre-otic muscles, post-otic myotomes invaded the territory in the same way as occurs ontogenetically in the case of the anterior trunk somites of Petromyzon (figs. 77 and 78). This evidence from Petromyzon meets an objection which may be raised against the theory, namely, that it is unreasonable to suppose that if the pre-otic region became too crowded to retain its own muscles it would be able to contain muscles from elsewhere, since this is precisely what seems to occur ontogenetically in this animal. In Petromyzon the pre-otic somites break up into loose mesenchyma and in later stages post-otic myotomes invade the territory. A comparison of figure 77 with figure 81, shows how similar the relations of the associated nerve in Petromyzon (*nv.* 2, fig. 77) and of the abducens nerve of Squalus are.

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McMurrich ('12) has recently advanced a theory (p. 175) which involves the assumption of this migration of post-otic myotomes into pre-otic relationships. Johnston ('02 and '05, pp. 230–233) has in my opinion completely refuted Fürbringer's argument in favor of the phylogenetic migration forward of trunk nerves and myotomes into the occipital region. To all who hold the view of the primary continuity of nerve and muscle the hypothesis will seem the only tenable one, in spite of obvious difficulties and objections. Belogolowy ('10 a, pp. 380–384) has recently advanced an extended argument against the hypothesis of the primary continuity of nerve and muscle.

The most obvious objection to this hypothesis is the entire lack of ontogenetic evidence in its support. Had the phylogenetic migration of muscle assumed by the hypothesis actually occurred, we should expect to find some ontogenetic evidence of it. But there is as little ontogenetic evidence that the somites from which the posterior rectus muscle develops have migrated from behind the ear as that the mandibular and hyoid arches with which they are associated topographically have migrated from a post-otic position into their present location in the embryo. Furthermore, the hypothesis cannot be reconciled with the fact that the abducens—a post-otic nerve—innervates a myotome (Van Wijhe's 2nd) of which a dorsal moiety is innervated by the trochlearis, a nerve with a pre-otic nidulus (fig. 81). The niduli of these two nerves lie in widely separated neuromeres of the brain—one of them pre-otic and one-post-otic—and yet they innervate muscles derived from the same somite. If the posterior rectus muscle were once post-otic, it is difficult to explain how the somite from which it is in part derived (Van Wijhe's 2nd) is innervated also by a pre-otic nerve with a pre-otic nidulus. If the hypothesis were true, it would be necessary to assume a migration of the nidulus of the trochlearis from behind the ear into its present position. Of such a migration of a motor nidulus from one metamere into another several segments removed, there is neither comparative anatomical nor embryological evidence. The careful comparative anatomical investigation of the nidulus of the abducens by Kappers ('10) discloses no such migration of the nidulus as McMurrich's

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hypothesis requires. On the other hand, there is much evidence of the distribution of motor nerves—such as the abducens—into metameres other than those in which they have their nidulus. This fact suggests a second hypothesis of the origin of the relations of the abducens to the posterior rectus muscle.

According to the second hypothesis, the abducens has attained its present relations by a process of substitution or nerve piracy; that is to say, a post-otic nerve has, in the course of phylogeny, usurped the area of distribution of a pre-otic one. The clue to the process by which this substitution has taken place is afforded by the anterior post-otic nerves in Petromyzon.

Ontogenetically, the two anterior post-otic somites of Petromyzon divide into median and lateral divisions, of which the former lie median to the otic capsule and adjacent to the notochord, while the latter lie lateral to the otic capsule and to the large ganglia of the ninth and tenth cranial nerves (figs. 78 and 79). The lateral portions of the myotomic divisions divide (completely, in the case of the first post-otic myotome) into a dorsal division (*my.* 4 *d.l.*), above the otic capsule, and a ventral division, below the ear, the division occurring along the line of lateral line sense organs. The relation between the series of lateral line sense organs—including the otic capsule—and the line of cleavage of the myotomic divisions seems more than merely topographic, and there is little reason to doubt that the development of the ear and the sense organs and their related ganglia has been one of the conditions—if not the essential condition—of the splitting of the myotomes. That is to say, the splitting of the myotomes may reasonably be regarded as an adaptation to the conditions brought about by the enlargement of the sense organs and cranial ganglia. The median division of the anterior post-otic myotomes develops embryonic muscle fibers, which degenerate and disappear in relatively early embryonic stages, for they are entirely absent in a 50 mm. embryo. With them disappear, it may be inferred, the associated somatic motor nerves; although, in spite of much pains, I have been unable to demonstrate the existence of embryonic nerves associated with these myotomic divisions. The reason for this fail-

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ure may perhaps be ascribed to the small size of lamprey embryos and the great difficulty of identification of embryonic nerves. The differentiation of muscle fibers, however, as Harrison has shown, does not imply the presence of nerves.

The portions of these myotomes lying lateral to the ear persist into the adult and form the anterior segments of the lateral trunk musculature (fig. 77; *my.* 4 *d.l.*, *my.* 4 *v.l.*). They are innervated by branches of nerves of posterior myotomes, namely, those of the fourth and fifth post-otic myotomes. That each of the anterior myotomes was at one time innervated by its own segmental somatic motor nerve seems indisputable, and some explanation of the present modified relationships seems required. We may assume that the nerve (*rx.v.*) (*n'v.* 1 and *n'v.* 2, fig. 77) which innervates the five most anterior post-otic myotomes consists of the combined nerves of these five segments, each of which retains its primary connection with its related myotome. This assumption harmonizes with the hypothesis of the primary continuity of nerve and muscle. Were this assumption correct, however, we should expect to find the nidulus of the nerve extending anteriorly as far as the otic capsule. Of this there is no evidence. The only neuroblasts, the processes of which can be traced into the roots of this nerve, lie solely in the region of the roots.

As an alternative explanation of the nerve and muscle relations under discussion, it may be assumed that the nerves associated with the three anterior myotomes have degenerated, while their area of distribution has been usurped by the nerves of posterior myotomes. The degeneration of the median division of the first post-otic myotome may have been one of the conditions which lead to this substitution in the case of this myotome. Such an assumption of nerve substitution is in harmony with the rapidly increasing evidence in favor of the process theory of nerve development and with the limitation of the nidulus of the nerve as stated above.

Furthermore, the evidence presented by Johnston ('08) and his conclusions, support this assumption. In his discussion of the segmental relations of ventral nerves in Petromyzonts John-

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ston writes (p. 584): "There seems to be no definite or constant arrangement of these motor fibers. They pass in a haphazard fashion to one or two myotomes, branch once, twice or three times, et cetera. In studying the peripheral nerves of Amphioxus with methylene blue I gained the general impression that the nerves in that animal showed still less regard for segmental relations." The point of these statements in this connection is, not the fact of irregularity of nerve relationships in these primitive chordates, but the evidence against the view of the inseparability of muscle and nerve, afforded by them. Such facts point unmistakably toward the possibility of changed innervation under changed conditions. Moreover, the more recent conclusions regarding the phylogeny of the nervous system (Parker '10) are against the view of the primary continuity of nerve and muscle.

Still further in confirmation of the view that the abducens has acquired its present relations by a process of substitution, is the fact to which my attention has been called by Dr. W. H. Lewis, that when the digastricus first arises in the human embryo it is innervated by the facial nerve. Later in development, the muscle divides and the anterior belly becomes innervated by a branch of the trigeminal. If such a process of nerve piracy occur ontogentically, it is clearly possible that a similar process may have taken place phylogenetically in the case of the abducens.

b. How may the innervation of musculature derived from two somites by a single nerve—the abducens—be best interpreted? The majority of investigators have confirmed Van Wijhe's statement that the musculature innervated by the oculomotor is derived from the first or pre-mandibular somite; that innervated by the trochlear is differentiated from the second or mandibular somite; while the abducens musculature is developed from the third somite. That is, each eye-muscle nerve is distributed to a single somite. With the exception of Dohrn ('01, '04) all students of the genesis of the eye muscles including Kastschenko ('88), Miss Platt ('91), Hoffmann ('97), Neal ('98), Sewertzoff ('99) and Lamb ('02), agree upon the monomyotomic distribution of these nerves. Belogolowy ('10 a, p. 252) finds that the anlage of the

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posterior rectus muscle in the chick consists of two or three masses, but he does not suggest that this division indicates a metamerism of the muscle.

Upon the basis of observations upon Torpedo embryos Dohrn ('90) inferred that each of the eye-muscle nerves has a polymeric origin and distribution, the abducens representing three or four metameres, the oculomotorius possibly a larger number, and the trochlear a single metamere. A year later, however, he concluded that the m. obliquus superior is developed from two myotomes. Regarding the number of somites in Torpedo, however, Killian ('91) and Sewertzoff ('99) reached conclusions divergent from those of Dohrn, and Dohrn ('91, '01, '07) has repeatedly revised his conclusions, and in his latest paper ('07) decides that the second somite of Van Wijhe represents three or four myomeres. In this connection the statement of Sewertzoff ('98) that the somites of Dohrn ('90) and Killian ('91) in Torpedo secondarily merge into those of Van Wijhe and that the myomeric segmentation of Torpedo and Pristiurus is identical, is important.

Miss Platt ('91) had noticed that just anterior to the anlage of the posterior rectus muscle there appears the rudiment of a large muscle derived from the posterior portion of the second (mandibular) somite. This muscle, according to Miss Platt, soon degenerates and her conclusion has been confirmed by Lamb ('02). Johnson ('13) thinks that he is able to identify the same rudiment in Chelydra embryos. But Dohrn ('01, '04) denies its degeneration and affirms its persistence as an integral part of the definitive posterior rectus muscle, the major portion of which is derived from the third somite of Van Wijhe.

Sewertzoff ('99) derives the posterior rectus muscle of the selachii from Van Wijhe's third somite, which he regards as the first true somite, and which he states is formed by the confluence of two primary somites. Sewertzoff makes the interesting discovery in Torpedo that the third and fourth somites unite to form the posterior rectus muscle. This divergence of opinion regarding the metameric relationships of the posterior rectus muscle is important and the whole problem should be reinvestigated in embryos of both Squalidae and Torpedinidae.

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After a careful reinvestigation of the genesis of the posterior rectus muscle the writer is able to affirm with positiveness that Dohrn ('01, '04) is correct in claiming the persistence of the rudimentary muscle which Miss Platt ('91) thought was transient in the embryo. On the contrary, it persists and forms, as Dohrn stated, the anterior portion of the posterior rectus muscle, and is innervated by the abducens nerve.

The problem presented by the fact of the distribution of the abducens nerve to two myotomes—Van Wijhe's second and third—is more apparent than real, since, as has been shown by Bardeen ('98) for mammals and by Johnston ('08) for Cyclostomes, a bimeric distribution is the rule for somatic motor nerves. Therefore, the distribution of the abducens to two myotomes, instead of presenting a difficulty, constitutes still further evidence of its morphological similarity with spinal somatic motor nerves.

c. Is the abducens of Gnathostomes homologous with the most anterior spinal nerves of Petromyzon? The cyclostomes have no posterior rectus muscle and no abducens nerve (Johnston '05 a). Assuming the primitive character of the cyclostomes, in this feature the conclusion seems inevitable, therefore, that in the course of phylogeny one or two of the anterior spinal nerves of the Cyclostomes have been converted into the abducens of the Gnathostomata. The apparent similarity between the ventral ramus of the anterior spinal nerves of Petromyzon (*n'v.* 2, fig. 77) and the abducens gives sufficient grounds for raising the question whether there may not be an homology—partial or complete—between them. The position attained by the musculature (*my.* 4 *v.l.*, fig. 77) innervated by the nerve *n'v.* 2 is so close to the eye as to make possible, through slight variations in the course of phylogeny, its attachment to the eye-ball. The nidulus of origin of both nerves is post-otic and somewhat extended, while the distribution is pre-otic. But here the resemblance ceases.

Against the exact homology of these nerves, it may be urged; first, that the myotome innervated by the abducens is a pre-otic one, while that innervated by the nerve *n'v.* 2 is a post-otic myotome; second, that the nerve *n'v.* 2 is the nerve of the fourth

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and fifth post-otic myotome while the fourth and fifth post-otic myotomes of Squalus (Van Wijhe's 7th and 8th) have their own somatic motor nerves, namely, the anterior roots of the embryonic hypoglossus (fig. 81), which must therefore be the exact homologues of the nerve *n'v.* 2.

The relations are such, however as to indicate that the abducens is the intrinsic nerve of Van Wijhe's 4th and 5th somites. The transient ramus recurrens of the abducens (VI, *rec.*, fig. 76) may possibly indicate the former relations of the abducens to the 6th somite or at least to posterior myotomes. If this conclusion be correct, then it follows that Petromyzon has, in the course of phylogeny, lost the homologue of the abducens with the loss of the median portions of the post-otic myotomes.

It will be recalled that the abducens has a ramus recurrens, observed by Dohrn ('90, '01), Miss Platt ('91), Neal ('98) and Belogolowy ('10), and interpreted by them as evidence of a former posterior distribution of the abducens. If this conclusion be correct, the homology of the abducens with the lost nerves of Petromyzon is rendered more certain.

One of Belogolowy's ('10 a) most important discoveries is the fact that in chick embryos the roots of the abducens and of the hypoglossus form members of a continuous series of anastomosing roots. By such evidence their serial homology seems clearly demonstrated. Moreover, he also finds roots of the abducens arising from the second hindbrain neuromere—a pre-otic neuromere—and infers that this root is a remnant of the primitive nerve belonging to the third somite. Belogolowy lays considerable stress upon the fact that anastomoses are formed between the abducens and the oculomotor fibers, resulting in relations resembling those between the abducens and the hypoglossus. Altogether the evidence seems overwhelming in favor of the view that all of these nerves form members of a continuous series of homologous nerves, and that the assumed distinction between post-otic and pre-otic regions of the head is arbitrary and artificial.

d. Conclusions regarding the morphology of the abducens. That the abducens is a somatic motor nerve innervating somitic mus-

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culature has been held on anatomical grounds by Bell ('30), Stannius ('49), Huxley ('74, '75), Schneider ('79), Gaskell ('86, '89), Strong ('90), Fürbringer ('97), Wiedersheim ('98), Gaupp ('99), Kappers ('10) and on embryological grounds by Van Wijhe ('82), Beard ('85), His ('88), Dohrn ('88, '90), Martin ('90), Oppel ('90), Zimmermann ('91), Miss Platt ('91), Hatschek ('92), Hoffmann ('94–'00), von Kupffer ('94), von Kölliker ('96), Neal ('96, '98), Sewertzoff ('98, '99), Carpenter ('06), Koltzoff ('01), Filatoff ('07), Belogolowy ('08, '10).

Relatively few morphologists have regarded the abducens as a splanchnic motor nerve. These are Stannius ('51) and Langerhans ('73) on the basis of the resemblance of the histological structure of the posterior rectus mucle to visceral musculature and Balfour ('78), Marshall ('81), Dohrn ('85) and Von Kupffer ('94) on embryological grounds.

Therefore on the basis of the strong preponderance of morphological opinion and on the ground that in its histogenesis, in its relations to a somatic motor nidulus and to somitic musculature, and finally in its histological structure the abducens resembles a somatic motor nerve no alternative view of its morphology seems possible. In its two divergent characters, namely, its lack of connections with sensory and sympathetic ganglia, the abducens shows primitive features which do not affect our conception of its morphology.

If, on the basis of the considerations presented above, there seem good reasons for thinking that the pre-otic and post-otic regions of the head were primitively alike and segmented in correspondence with a somitic musculature, the question naturally arises whether the eye muscle nerves and their relations throw any light upon the vexed question of the number of cephalic segments. The demonstration of a segmented somitic musculature with associated somatic motor nerves in the head region would seem to warrant an optimistic view of the possibility of a definite answer to the problem with which morphology has wrestled without cessation for over a century. We may therefore turn to the following question:

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5. How many metameres are represented by the three eye-muscle nerves?

It was the undisputed opinion of the earlier morphologists that each of the eye-muscle nerves represented a single metamere. As long as vertebrate morphology was largely based upon anatomical data, or at least the leading morphologists were comparative anatomists, there appeared little reason for assuming a polymerism of these nerves. Each was considered a segmental nerve or the ventral root of a segmental nerve and that conception met all intellectual demands.

When, however, comparative embryology developed, the discovery of a cephalic coelom and an independent mesodermic segmentation in the head region of elasmobranch embryos drew investigators away from anatomy, and the history of the head became written largely in terms of ontogenesis. Competition arose among embryologists to determine who could discover the largest number of ancestral head segments; and somites, neuromeres and epibranchial placodes became successively the favorite objects of investigation. The need of motor nerves to supply these segments soon became apparent and all evidence of polymerism of nerves was eagerly sought.

Dohrn ('90), upon the discovery of more numerous mesodermal segments in Torpedo embryos than had been discovered elsewhere, became a strong advocate of the polymerism of the eye-muscle nerves. For it was evident that the morphological importance and segmental value of his mesodermic segments in large measure depended upon the demonstration of a corresponding segmentation of other organ systems. However, objections were quickly raised to throw doubt upon the real metameric value of Dohrn's mesodermic segments. It was soon found that some of the microcoelic cavities which Dohrn had called somites were merely transient vesiculations of the mesoderm of the mandibular arch ventral to the somitic mesoderm; that the segments did not correspond upon the two sides of the body (an objection to which Dohrn replied that it was to be expected in degenerating structures); that the segments are not constant, as evinced

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by the divergence in the results of different investigators—Dohrn ('90), Killian ('91), and Sewertzoff ('98, '99); that similar microcoeles are seen in the trunk region but that they soon become confluent to form the definitive somites, just as in the head region they unite to form the somites of Van Wijhe (Sewertzoff '98, '99); that they lack numerical correspondence with other metameric structures; that they appear only in a divergent and highly modified group of elasmobranchs—the Torpedinidae; and that they may be considered of metameric value only by ignoring the evidence from comparative anatomy.

Notwithstanding all the objections raised against their metameric worth, Dohrn regarded them as the essential criteria of the primitive segmentation of the vertebrate head, and he considered this opinion supported by evidence of the polymerism of the eye-muscle nerves. Gast ('09) shares with him this conception of their value on the ground (p. 424) "that the polymerism of the hyoid and mandibular arches is attested not only by the different cavities of their mesodermic segments but by the strong evidence of the polymerism of the nerves associated with them." Brohmer ('09, p. 39) objected to Dohrn's conclusions on the ground that although it is necessary to assign a nerve to each 'primitive segment' of the head, Dohrn had left this anatomical standpoint out of consideration. The truth of this assertion is emphatically denied by Gast ('09) who affirms that Dohrn did not disregard the innervation of the mesodermic segments. Gast accuses Brohmer of being only superficially acquainted with Dohrn's argument for the polymerism of the trochlear and the abducens. Brohmer, however, is not the only morphologist who is skeptical of the real existence of the 'nerves' which Dohrn associates with his numerous mesodermic segments. As a matter of fact the foundation for Dohrn's assumption of the polymerism of the eye-muscle nerves, namely, the polymerism of Van Wijhe's somites, is denied.

Dohrn bases his inference of the polymerism of the trochlear on the assumption that the mandibular cavity is polymeric; that the trochlearis divides into two branches; that there are two hindbrain neuromeres corresponding to the two trochlear nerves;

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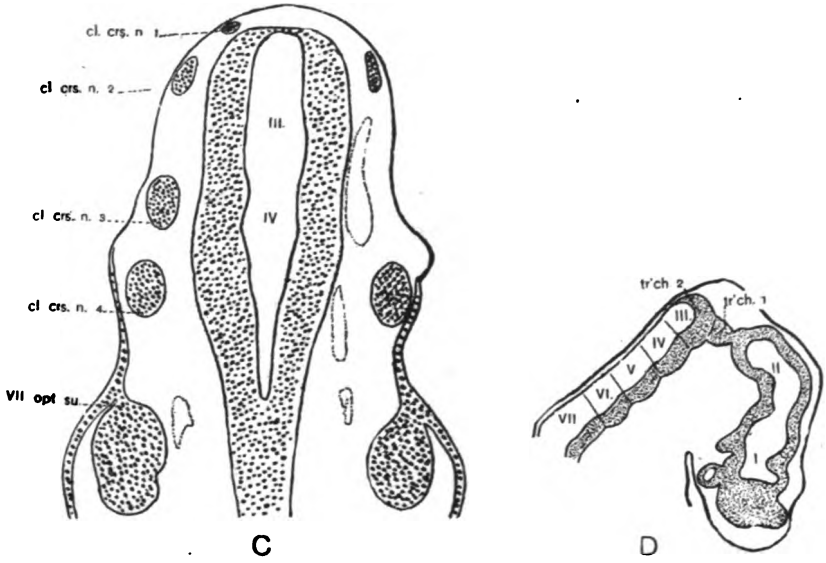
and that there are in Torpedo marmorata two transient ganglia associated with the trochlear anlage. Text figures C and D illustrate Dohrn's argument. Corresponding with the four mesodermic segments which he claims are represented in the mandibular cavity Dohrn discovers two 'trochlear neuromeres' (*tr'ch.* 1; *tr'ch.* 2) and two trigeminal neuromeres (IV and V). The



Text fig. C Horizontal section of a 9 mm. embryo of Torpedo marmorata, after Dohrn ('07); *cl.crs.n. 1*, 'chiasma' group of cells; *cl. crs.n. 2*, anterior 'trochlear ganglion;' *cl.crs.n. 3*, second 'trochlear ganglion;' *cl.crs.n. 4*, Gasserian ganglion; *VII.opt.su.*, ganglion of the r. ophth. sup. facialis; *III, IV*, Neal's neuromeres.

Text fig. D A parasagittal section of an embryo of Torpedo, after Dohrn ('07); *I–VII*, neuromeres according to Neal ('98); *tr'ch. 1, tr'ch. 2*, Dohrn's trochlear neuromeres; *IV, V*, Dohrn's trigeminal neuromeres; *VI*, Dohrn's facialis neuromere.

two 'trochlear ganglia' found in Torpedo are seen in the frontal section represented in figure 3.

In support of the contention that the second myotome is polymeric and corresponds to at least two myotomes, Dohrn mentions the fact that from this myotome are differentiated two

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muscles innervated by two independent nerves, the abducens and the trochlear. This evidence alone, however, does not necessarily warrant the conclusion drawn by Dohrn, since each myotome is typically innervated by two somatic motor nerves. Further, the two myotomic divisions of the mandibular cavity are not antero-posterior in their relations, as Dohrn's hypothesis would require, but are dorso-ventral in their relations to each other.

Since it would be difficult to find any somatic motor nerve which does not divide into at least two branches, this fact does not materially strengthen Dohrn's polymeric assumption.

The second of Dohrn's trochlear neuromeres is a late secondary subdivision of the most anterior hindbrain neuromere. From the evidence of a purely topographic relation with a clump of disintegrating neural crest cells, Dohrn infers that the trochlear includes the splanchnic motor niduli of two metameres. Unfortunately for this supposition, however, Dohrn is unable to demonstrate the presence of these two niduli. He states that no splanchnic motor fibers persist in connection with the second trochlear neuromere. Here again he is in error, since the splanchnic motor fibers of the ramus mandibularis trigemini have their nidulus in this portion of the hindbrain. These fibers enter the brain as the minor root of the trigeminal. If Dohrn's scheme of segmental relations were correct, two splanchnic motor nerves—his 'second trochlear' and the ramus mandibularis trigemini would have their niduli within the same neuromere—Dohrn's 'second trochlear' neuromere. These nerves actually do have their niduli in a single neuromere (neuromere III—Dohrn's first and second trochlear) but one has a nidulus in the somatic motor column while the other has a splanchnic motor nidulus. The weakest point in Dohrn's argument is its failure to take into consideration the central nidular relations. The argument in favor of the polymerism of the trochlear seems unconvincing, although it is the strongest argument yet advanced with this purpose in view. The argument in favor of the polymerism of the oculomotor is even less adequate.

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In objection to Dohrn's conclusions Belogolowy ('10 b, p. 23) advances the following considerations:

> Dohrn, on the basis of the plurality of the ganglionic clumps connected with the trochlearis anlage and the subdivision of the nerve into single fibers, inferred the plurality and polymerism of the trochlearis. The discoveries of Dohrn appear to me quite insufficient to draw such a conclusion from, since it is impossible to use as a basis for such inferences the plurality of position and number of such indefinite elements. Were we to follow this method, it would be easy as the final result to consider the maximum number of branches which might be met by chance as the number of segmental nerves which have participated in the formation of the trochlearis; and the presence of clumps of neural crest cells which accompany these branches might be considered as sufficient proof of our assumption. But it appears to me at least risky to admit as a decisive criterion for our inferences the accidental occurrence of this or that number of anastomoses or ganglionic clumps.

On the other hand, there appear good reasons for regarding the abducens as a nerve representing more than a single metamere. In the first place its roots arise from at least two hindbrain neuromeres (neuromeres VII and VIII) and its nidulus is equally extensive; its transient and rudimentary ramus recurrens is suggestive of an earlier distribution to posterior myotomes; and lastly, it is distributed to myotomes other than those of its own metamere.

It might seem at first thought as if the most convincing evidence bearing upon the question of the polymerism of the abducens and the other eye-muscle nerves is the simple fact that they are distributed to three successive myotomes, Van Wijhe's first, second and third. And were this the only relation to be taken into consideration, such a conclusion would seem unavoidable. This conclusion however conflicts with the evidence that at least three neuromeres separate the niduli of the trochlear and abducens; and, further, the evidence that the abducens innervates muscles of other metameres than those of the post-otic metamere to which it belongs. Therefore the problem of the number of metameres represented by the three eye-muscle nerves cannot be solved by ignoring the neuromeric relations.

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Ziegler ('08) and his pupil Brohmer ('09) have recently attempted to determine the number of cranial metameres, ignoring the neuromeric segmentation. Is neuromerism a matter of no consequence to the student of head morphology?

6. Are neuromeres satisfactory criteria of the primitive metamerism of the head?

By his discovery of symmetrical cross furrows on the widely expanded neural plate of Salamandra atra embryos von Kupffer became the first exponent of the view that the nervous system manifests a 'primary metamerism,' independent of the mesodermic segmentation. He was the pioneer—as he was in many other lines of morphology—among those who lay stress upon the segmentation of the nervous system as the best preserved manifestation of the primary metamerism of the vertebrate body. Repeated confirmation of the presence of neural segments prior to the appearance of mesodermic segmentation has been given by Froriep ('91, '93), Locy ('95), Hill ('00), Johnston ('05), Wilson and Hill ('07) and Griggs ('10).

At the same time it is a truism of morphology that the segmentation of the nervous system is a secondary one, determined by and dependent upon the segmentation of the muscular system. This has been especially emphasized by Mihalkowitz ('77), Ahlborn ('84 b), Froriep ('92), Kingsley ('12) and Coghill ('13). Observation, however, seems to have warranted the generalization that the nervous system is most conservative. When once it has acquired a segmentation adapted to whatever peripheral system, the segmentation is retained, even after the associated structures, sensory or muscular, have disappeared. So that when it was demonstrated beyond a doubt that the hindbrain neuromeres manifest a segmentation which could not be interpreted upon purely mechanical grounds and which appear independently of the mesodermic segmentation, the conclusion seemed inevitable that in these hindbrain neuromeres is preserved the indisputable remnants of the primary segmentation of the head. Finally when Locy ('95) claimed to have been able to trace the

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'primary' neuromeres of the open neural plate of selachian embryos into the neuromeres of the closed neural tube, it seemed as if neural segmentation were the court of last appeal in all questions relating to the ancestral metamerism of the head. Few morphologists—Mihalkowitz ('77), Broman ('95), and Filatoff ('07)—have held the neuromeres to be purely the results of mechanical pressure or of growth in confined space and devoid of phylogenetic significance. This interpetation has been discredited since the demonstration that the hindbrain neuromeres of many vertebrate embryos are local thickenings of the medullary wall and not defined merely by foldings of the wall.

Johnston ('05, p. 234) probably expresses the general attitude of morphologists when he says that "nervous structures represent more segments than have been preserved in the mesoderm. In other words, there are preserved vestiges of nerve structures belonging to segments whose entodermal and mesodermal organs have disappeared for the most part. But the division of the brain wall into neuromeres gives a clue to the number of segments." The same implicit confidence in the value of the subdivisions or segments of the nervous system as criteria of the primitive metamerism is expressed by Griggs ('10, p. 434) in the conclusion that "if, as the most recent investigation seems to show, the nervous system, appearing first, presents a simpler and more unaltered condition than the other two systems, then it may well serve as a basis for the study of the segmentation of the head; and other organs should be shown to correspond to it rather than vice versa." It may well be doubted, however, if the truth of the premises of either Johnston or Griggs may be admitted.

Notwithstanding the faith inspired in these morphologists that, through the study of neuromerism the primary metamerism of the head will be ascertained, the conflict in their observations and conclusions seems hardly to justify their confidence. In the Urodeles, for example, Kupffer ('85) finds eight primary neuromeres in the region where Froriep ('91, '93) finds three, or four, or five, and an anterior unsegmented region large enough to include three or four more. Froriep, however, denies their seg-

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mental value. Eycleshymer ('95) also finds only a few large segments of no metameric significance. Locy ('95) found four or five in the region and agreed with Froriep and Eycleshymer that they were of no segmental importance. Griggs ('10) recognized one neuromere in the forebrain region, two in the midbrain and one or more in the hindbrain region and regards these as the only true neuromeres. On the other hand, there are "in the closed neural tube of Amblystoma a series of swellings, extending from the anterior end of the brain to the otic pit, but since these divisions are of varying morphological significance they cannot rightly be called neuromeres." By what criteria shall the real neuromeres be determined? Is Griggs correct in denying neuromeric value to the forebrain or midbrain vesicles or their secondary subdivisions? Are the true neuromeres those of the open neural plate of Amphibia, as Griggs maintains, or are the real neuromeres those of the closed tube as held by the majority of morphologists? The difficulty of determining the real metamerism of the nervous system is increased, if morphological opinions are influenced at all by the segmentation of the brain of Bdellostoma.

Dr. Bashford Dean, in a letter which he kindly permits me to use, makes the following statement of the neuromeric conditions in Bdellostoma embryos:

> If we believe that a 'neuromere' is represented objectively by a specially and definitely dilated spot in the central nervous system, expressed either in the inner lumen or in the outer wall of the medullary axis, we certainly cannot interpret the conditions in the hag-fish in terms, for example, of the shark or the amphibian. In the first place, the hag-fish embryos may show a great number of these dilated regions, as many indeed as twenty-seven or twenty-eight in the midbrain and hindbrain. They may indicate also that these dilated areas are indefinite in number; and that in relatively the same age these areas may be either very obscure, absent, or barely visible, or may be reckoned with almost mathematical precision. They are moreover, rarely symmetrical; it is curious also that their symmetry is never expressed in the same way in the large series of embryos examined. Neuromeres are difficult to distinguish in the forebrain of Bdellostoma. Occasionally there appear to be two, three, or four present. These can be discerned faintly on one side or the other side of the medullary axis, never paired.

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In the midbrain as many as eight may be reckoned, and in other embryos none at all. A symmetrical number sometimes occurs. In the cases just examined, I find five specimens out of fourteen showing the same number of midbrain neuromeres on both sides. In one case I counted three right, three left; in another eight right, eight left; in another three right, three left; in another four right, four left, and finally one in which but a single neuromere appeared on either side. In the hindbrain, the number of neuromeres varies between three and twenty-four, and they differ in number on different sides, a difference of ten having been noted in the same individual in right and left sides of the body.

It may be objected of course, (1) That in these cases of asymmetry the neuromeres were present on the 'off' side but were 'suppressed,' and therefore could not be counted. (2) That the change in the number of neuromeres might be due to different stages in development, the neuromeres appearing most completely at a definite date of development. The fact remains, nevertheless, that asymmetry and variable numbers are present, and to an extraordinary degree, a state of affairs which does not make in the direction of clearing up our knowledge of these 'segmental' structures. (3) That the neuromeres of Bdellostoma are artifacts. Against this criticism I note that I have seen them clearly in living embryos.

But it may be objected that the foldings of the Bdellostoma brain are not the symmetrical foldings which have been recognized as neuromeres in other forms; that no one would be likely to interpret the variable and asymmetrical structures which Dean describes in Bdellostoma as of phylogenetic or morphological value; that real neuromeres are symmetrical and permanent thickenings of the brain wall. In reply to such objections it should be remembered that morphologists have not always insisted upon the constancy or the symmetry of problematic structures. In fact Dohrn ('04), in reply to this objection to his microcoelic mesodermic segments, replied that inconstancy and asymmetry would be expected in degenerating metameric structures like these. Out of hundreds of Squalus embryos examined by the writer in order to confirm Locy's results only two or three showed symmetry or regularity in the segmentation of the edges of the neural plate (figs. 2 and 3, Neal '98). Yet morphologists have not refused to accept Locy's conclusions because of this lack of confirmation of his results on selachians.

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The main objection to the use of neuromeres as essential criteria of metamerism is not so much their variability in different vertebrates or the diversity of opinion among morphologists regarding them, as it is the difficulty of finding criteria by means of which the coenogenetic may be distinguished from the palingenetic, especially in the regions of the forebrain and hindbrain. In an earlier paper ('98) the writer protested against the uncritical acceptance of all sorts of foldings of the central nervous system—dorsal, ventral or lateral—as evidence of the primary metamerism of the nervous system. Special protest was raised against the claim of Locy ('95) that he had been able to trace the 'primary' neuromeres of the open neural plate into the neuromeres of the closed neural tube. Eycleshymer ('95) and Kingsley ('97) were likewise unable to accept Locy's assertions.

Hill ('00), however, confirmed Locy's results by his observations on teleost and chick embryos and considered Neal's objections as 'negative.' Wilson and Hill ('07, p. 147) on the other hand "cannot admit that Hill has fully and adequately met Neal's objections to Locy's interpretation of the early crenation of the margin of the cephalic plate, for example, in Squalus. The weightiest part of Neal's contention, as it appears to us, is not merely negative, as C. Hill represents it, but resides in the positive statement that the beaded thickenings found are not only asymmetrical but are quite variable in different specimens."

Johnston ('05), ignoring Neal's objections, accepts the results of Locy and Hill on the ground that "the work of these last two authors is evidently most painstaking and their results are so complete and so far in agreement that they may be taken to represent the present state of knowledge of the neuromeres." Yet von Kupffer ('06, p. 164), working on chick embryos, finds that Hill's 'astonishing pictures' of the neuromeres of the chick give the impression that "the subjective motive of the investigation had influenced too much the completion of the drawings." Kupffer states (p. 248) that in spite of equally extended observations he was not able to confirm Hill's results. Gräper ('13) also has been unable to find Hill's neuromeres in the chick.

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Therefore, in view of the disagreement among students of neuromerism regarding the nature and number of true neuromeres, and the persistent doubt regarding the results of Locy and Hill, morphologists may still feel skeptical regarding any scheme of metamerism based upon the segmentation of the nervous system and uncontrolled by the evidence of mesodermic segmentation.

The writer finds himself in agreement with Belogolowy ('10 a, p. 510) in the opinion that the neuromeres have only a secondary importance as criteria of the primitive segmentation of the head. The latter states (p. 515) that:

> Without having any organic relations to the functional activities of the nervous system, and presenting merely form changes of the neural tube, the neuromeres in my opinion, can serve at best merely as topographic landmarks in the study of the nervous centers. The complete lack of any satisfactory explanation of their appearance and the indications of the possibility of their purely secondary formation under the influence of this or that mechanical factor acting on the nervous system—as in the case of the constrictions of the spinal cord under the pressure of the somites—limits to the utmost their employment as criteria of metamerism.

Johnston's assertion ('05, p. 234) that "nervous structures represent more segments than have preserved in the mesoderm;" that "in other words, there are preserved vestiges of nerve structures belonging to segments whose entodermal and mesodermal organs have disappeared for the most part" begs the entire question. The fact that the brain shows a larger number of divisions—whether the problematical marginal beadings of Locy or the secondary subdivisions of the differentiated tube—than does the mesoderm, does not prove that the nervous divisions are ancestral or primitive. Moreover, there is no reason for assuming that mesodermic segments have disappeared in the head region of Squalus. As a matter of fact, the number of somites in Squalus corresponds with the number of primary brain vesicles. In this numerical correspondence we have the strongest proof of the metameric value of these two segmental structures. Moreover, this inference accords more fully with the conclusions

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of comparative anatomy than does the assumption of more numerous pre-oral segments.

Assuming on such grounds the metameric value of those primary brain vesicles or neuromeres which correspond numerically with the somites of Van Wijhe, more metameres are found anterior to the ear than are admitted in the schemes of metamerism of Ziegler and Brohmer, but fewer than in those of Johnston and Belogolowy. In figure 76 are diagrammatically expressed the primitive segmental relations based on the assumption of a correspondence of primary neuromeres and Van Wijhe's somites. That the abducens may be regarded as the somatic motor nerve of a metamere posterior to the one whose myotome it innervates seems indicated by its relations. Neuromeric relations therefore afford an important clue to the primitive metameric relations of the head. For this reason neuromeric segmentation may not be disregarded in any attempt to define the metamerism of the head.

7. Are these metameres serially homologous with those of the trunk?

A summary of the evidence gathered by the last two generations of vertebrate morphologists convincingly demonstrates that the vertebrate head possesses a metamerism comparable with that of the trunk. First and most important, a true somitic segmentation occurs in pre-otic and post-otic regions alike. An identical segmentation characterizes selachian (Van Wijhe '82), amphibian (Miss Platt '97) and cyclostome (Koltzoff '01) embryos. That is to say, these craniotes pass ontogenetically through an acraniate stage, comparable to the adult form of Amphioxus.

The discovery by Koltzoff ('01–'02) that in embryos of Petromyzon a series of somites—exactly homologous with those discovered by Van Wijhe ('82) in selachian embryos—occurs, not a single one of which disappears in ontogeny so that the muscular metamerism is unbroken as in Amphioxus, appears to the writer to be one of the most important made during the present generation. The recent rehabilitation of Amphioxus as an ancestral type by Delsman ('13) seems to justify the hope that

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the ancestral history of the head may yet be known and general agreement among morphologists be attained.

In both pre-otic and post-otic regions of the body the mesodermic corresponds numerically with the neuromeric segmentation. While the topographic alternation is not clear in the head as in the trunk, the relations, both nervous and numerical, indicate a primitive correspondence.

The somatic motor column continues uninterruptedly from post-otic into pre-otic regions. In both regions nervous connection with somitic musculature is effected similarly by the movement of the protoplasm of the neuroblasts lying in that column. The secondary connection of nerve and muscle in both regions affords the possibility of the acquisition of new metameric relations such as appear in the case of the abducens nerve. The relations of this post-otic nerve to pre-otic myotomes indicates that no fundamental difference distinguishes the two regions.

The somatic motor nerves acquire relations with somatic sensory nerves and with sympathetic anlagen in the pre-otic region in precisely the same manner as do spinal somatic motor nerves. The misinterpretation of these relationships has long obscured the perception of their true morphology and delayed the acceptance of the conclusion that head metameres are comparable with those of the trunk.

Typical pre-otic metameres, represented by the midbrain-oculomotor-premandibular and by the hindbrain-trochlear-mandibular segments, possess all of the essential components of typical trunk metameres, namely, myotome, sclerotome, neuromere, somatic motor and somatic sensory nerves, and sympathetic anlagen. Their morphological comparability can be doubted only by doubting facts which have been repeatedly confirmed. Neither comparative anatomy nor embryology justify the speculation that these elements are of exogenous, post-otic origin.

Over against such evidence, we have differences between pre-otic and post-otic regions such as would be expected in highly differentiated regions. But the considerations advanced above indicate that these differences are differences of detail and are not fundamental. They would appeal more strongly as objec-

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tions to those not fully conversant with the embryos of selachians and cyclostomes, or those whose views are affected by some divergent view of the ancestry of vertebrates. Ontogenesis strongly favors the view that the metamerism of the vertebrate body extends throughout its length and that the metameres of the head are morphologically similar to those of the trunk.

8. *The primary segmentation of the pre-otic region: Conclusions*

The evidence presented in the present paper scarcely justifies the attempt to draw conclusions regarding the maximal number of pre-otic metameres. Admirable attempts in this direction have recently been made by Johnston ('05 a) and Belogolowy ('10 a). The writer is convinced, however, in the light of the evidence now at hand that we may make positive assertions as to the minimal number of pre-otic segments, and as to their essential constituent elements.

The vertebrate head anterior to the ear consists of at least five metameric divisions, diagrammatically represented in figures 73 to 76. Their more important constituents may be summarized as follows:

The most anterior pre-otic metamere contains a well defined mesodermic segment, the anterior somite of Miss Platt ('90), the early degeneration of which is correlated with the absence of a somatic motor nerve in this metamere. The homology of this somite with the adhesive organ of Amia (Reighard '02) does not invalidate the comparison with a trunk somite, however surprising such a modification of a somite may appear. The absence of a sympathetic ganglion is to be expected in a metamere devoid of a motor nerve. The nervus terminalis appears to be the somatic sensory element of the segment. The writer agrees with Belogolowy ('10 a) in regarding this as the primary nerve of the olfactory apparatus, and its ganglion the primary ganglion of the olfactory nerve.[2] Burckhardt's assertion that the nervus terminalis of selachians contains motor fibers needs con-

[2] Brookover has recently confirmed this opinion on the basis of observations upon Amia embryos.

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firmation. The neuromere of the first cephalic metamere is the primary forebrain vesicle. None of the secondary subdivisions of the vesicle are morphologically comparable with hindbrain neuromeres. Notwithstanding the fact that morphologists, including Dohrn, von Kupffer, Johnston, and Belogolowy, assume a larger number of segments in this region of the brain, the writer is unable to accept their conclusions as well-founded. They rest upon evidence of equivocal neuromeres, doubtful nerves, problematic microcoelic cavities, the walls of which Dohrn has called somites, upon the far-fetched homology of the eye with dorsal ganglia and other debatable grounds. The so-called thalamic nerve is simply a persistent strand of neural crest cells which never shows neuroblast nor fiber. If it have any phylogenetic significance at all, it is not to be regarded as evidence of an additional member of the series of somatic sensory nerves, but as the old cellular root of the profundus nerve, the fibers of which now enter the brain along the profundus commissure and through the Gasserian ganglion. An optic neuromere is recognized by Johnston and Belogolowy on the debatable ground of the homology of the optic vesicle with a portion of the neural crest. In view of the doubt regarding the phylogenesis of the paired and the pineal eyes and the great uncertainty whether the former were primitively dorsal or ventral, the comparison of these structures with the anlagen of ganglionic nerves and with each other appears decidedly premature.

The assumption of Hoffmann ('94) that the anlagen of the ganglionic nerves are hollow outpocketings of the neural tube is a concept rather than a percept. No one has ever seen in sections of well preserved embryos the neural crest appear as hollow outpocketings with a lumen continuous with that of the tube. The basis for such a conception as that of Hoffmann consists of the doubtful evidence of two layers of cells in the nerve anlagen. The lumen is a product of the imagination.

Moreover, it is not so certain as would be desirable for a confirmation of the hypothesis that the paired eyes were primarily dorsal structures. The lowest vertebrates—including Amphioxus in that category—show the eye as a ventral or lateral structure

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and not as a dorsal one (Parker '08). Granting the fact that vertebrates have existed—and still exist—with eyes near each other and the median plane, the evidence that this was the primitive relation is wanting.

In the light of the evidence now in our possession, all that may be affirmed with assurance with regard to the metamerism in the forebrain region is that in this region we have at least a single metamere, serially homologous with those of the trunk. The morphologist who goes farther than this and affirms the polymerism of the forebrain segment is skating on extremely thin ice.

The elements of the second metamere are shown in the diagrammatic cross-section represented in figure 73. The myotome is the premandibular and the neuromere the midbrain. The somatic sensory nerve is the ophthalmicus profundus and the sympathetic ganglion is the ciliary. That the ophthalmicus profundus trigemini was once an independent segmental nerve seems evinced by its relations in cyclostomes. The secondary splitting of the premandibular myotome into dorsal and ventral moieties is evidently correlated with the development of the eyeball (fig. 81). The facts do not warrant the assumption of some morphologists that the oculomotor nerve—the somatic motor nerve of this metamere—has a bimeric distribution. No one who has made this assumption has been able to demonstrate the required two motor niduli. The premandibular somite is a single somite. The slight ventral fold in the wall of the midbrain is not sufficient evidence to establish the existence of two neuromeres. The large size of this neuromere, as well as that of the forebrain, is correlated with the functional importance of these portions of the brain. Their later subdivisions may be best interpreted as coenogenetic.

The third metamere consists essentially of the elements shown in figures 75, 76 and 81. Its myotome is the mandibular and its neuromere the cerebellar (neuromere III), within which lies the nidulus of the trochlear nerve, which is therefore the somatic motor nerve of the segment. The trochlear nerve becomes connected with the ramus ophthalmicus superficialis trigemini, the somatic sensory nerve of the metamere. There is evidence of

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a transient sympathetic anlage. While the chiasma of the trochlear is an anomaly, it may be regarded as coenogenetic and its existence does not invalidate the comparison of this metamere with a trunk segment. The ramus mandibularis trigemini appears to be the splanchnic motor element of this metamere.

The fourth metamere contains the third or hyoid myotome and the fourth neuromere (second hindbrain neuromere). To this segment may be assigned as the somatic sensory nerve the major root of the trigeminal in part. Since no neural crest is proliferated from this neuromere, however, this assignment must be made with a question mark, although the major root of the trigeminal is attached to this neuromere. The neuroblasts in the somatic motor column of this neuromere do not produce a nerve. The transient nerve seen in this region in chick embryos (Belogolowy '10) may be the somatic motor nerve of this metamere which has disappeared phylogenetically. The myotome of the metamere, however, is innervated by the nerve of a post-otic metamere, the abducens. An attempt has been made above to explain this anomalous relationship which does not appear to vitiate the comparison with a trunk metamere.

The fifth and last pre-otic metamere includes the fifth neuromere and the fourth somite which is partly sub-otic, a position to which it presumably owes the loss of its myotome. To the degeneration of the myotome may be attributed the loss of the somatic motor nerve of this metamere. No sympathetic anlage develops in this segment and the somatic sensory components are also lost. But the proliferation of the cells of the facialis nerve from this neuromere justifies the inference that they once have been present in this nerve. The loss of the myotome of this and of the following somite, a loss in all probability due to the enlargement of nerve ganglia and sense organ in this region, tends to show that the preservation of the myotomes of the first, second and third somites is due to their functional relation with the eye-ball. The eye muscles are the last remnants of the lateral trunk musculature anterior to the ear. Their earlier relations with post-otic myotomes are diagrammatically expressed in figure 81.

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LITERATURE CITED

AHLBORN, F. 1884 a Ueber den Ursprung und Austritt der Hirnnerven von Petromyzon. Zeit. wiss. Zool., Bd. 40.

1884 b Ueber die Segmentation des Wirbelthierkörpers. Zeit. wiss. Zool., Bd. 40.

ALLIS, JR., E. P. 1889 The anatomy and development of the lateral line system in Amia calva. Jour. Morph., vol. 2.

1897 The cranial muscles and cranial and first spinal nerves in Amia calva. Jour. Morph., vol. 12.

1902 The lateral sensory canals, the eye muscles, and the peripheral distribution of certain of the cranial nerves of mustelus laevis. Quart. Jour. Micr. Sci., vol. 45.

ALTMANN, R. 1885 Bemerkungen zur Hensen'schen Hypothese von der Nervenentstehungs. Arch. Anat. u. Phys. 1885.

ANDERSON, H. K. 1903 Reflex pupil-dilatation by way of the cervical sympathetic nerve. Journ. Phys., vol. 30.

VON APATHY, S. 1889–1890 Nach welcher Richtung hin soll die Nervenlehre reformirt werden? Biol. Centralbl., Bd. 9.

1897 Das leitende Element des Nervensystems und seine topographische Beziehungen zu den Zellen. Mitth. Stat. Neapel., Bd. 12

1898 Ueber Neurenfibrillen und über ihre nervös leitende Natur. Proc. Inter. Cong. Zool., 1897.

1907 Bemerkungen zu den Ergebnissen Ramón y Cajals hinsichtlich der feineren Beschaffenheit des Nervensystems. Anat. Anz., Bd. 30.

APOLANT, H. 1896 Ueber die Beziehung des Nervus oculomotorius zum Ganglion ciliare. Arch. f. mikr. Anat., Bd. 47.

ARNOLD, F. 1831 Der Kopftheil des vegetativen Nervensystems beim Menschen, in anatomischer und physiologischer Hinsicht bearbeitet. Dissertation, Heidelberg.

AYERS, H. 1892 Vertebrate cephalogenesis. II. A contribution to the morphology of the vertebrate ear, with a reconsideration of its functions. Jour. Morph., vol. 6.

BACH, L. 1896 Ueber die Localisation der Oculomotoriuskerne. Neur. Centralbl., Bd. 15.

VON BAER, K. E. 1828 Ueber Entwicklungsgeschichte der Tiere. I. Konigsberg.

BALFOUR, F. M. 1877 a On the development of spinal nerves in elasmobranch fishes. Stud. Physiol. Lab. Univ. Cambridge. Also in Philos. Trans. Roy. Soc., 1875.

1877 b Development of the spinal nerves and the sympathetic nervous system. Jour. Anat. and Physiol., vol. 11.

1878 A monograph on the development of elasmobranch fishes. London.

1881 A treatise on comparative embryology. London.

BARDEEN, C. R. 1898 The development of the musculature of the body-wall in the pig, including its histogenesis and its relations to the myotomes and to the skeletal and nervous apparatus. Johns Hopkins Hosp. Reports, vol. 9.

Digitized by Google

BARDEEN, C. R. 1903 The growth and histogenesis of the cerebro-spinal nerves in mammals. Am. Jour. Anat., vol. 2.
1904 The bimeric distribution of the spinal nerves in elasmobranchii and urodela. Am. Jour. Anat., vol. 3.

BARKER, L. F. 1899 The nervous system and its constituent neurones. New York.

BEARD, J. 1884 On the segmental sense organs of the lateral line and on the morphology of the vertebrate auditory organ. Zool. Anz., Bd. 7.
1885 The system of branchial sense organs and their associated ganglia in Ichthyopsida. A contribution to the ancestral history of vertebrates. Quart. Jour. Micr. Sci., vol. 26.
1888 Morphological studies. II. The development of the peripheral nervous system of vertebrates. Quart Jour. Micr. Sci., vol. 29.
1892 The histogenesis of nerve. Anat. Anz., Bd. 7.
1896 The history of a transient nervous apparatus in certain Ichthyopsida. Zool. Jahrb., Abt. f. Anat., Bd. 9.

BELL, C. 1830 The nervous system of the human body. Papers delivered to the Royal Society of London. London.

BELOGOLOWY, J. 1908 Zur Entwickelung der Kopfnerven der Vögel. Ein Beitrag zur Morphologie des Nervensystems der Wirbeltiere. Bull. Soc. Imp. Moscou, Hft., 3 und 4.
1910 a German reprint, Moscou.
1910 b Une branchie prespiraculaire chez le triton. Sur la question de l'origine de la bouche des vertebres. Biol. Zeitschr., Bd. 1.
1910 c Studien zur Morphologie des Nervensystems der Wirbeltiere. Die Entwickelung der Nervus trigeminus Gruppe bei Reptilien. Bull. Soc. Imp. Moscou. Bd.

BERANECK, E. 1884 Recherches sur le développement des nerfs craniens chez les lizards. Rec. Zool. Suisse, tom. 1.
1887 a. Étude sur les replis medullaires du poulet. Rec. Zool. Suisse, tom. 4.
1887 b Histogenese des nerfs cephaliques. Arch. sci. nat. Geneve, tom. 17.

BERNHEIMER, S. 1897 Ein Beitrag zur Kenntniss der Beziehungen zwischen dem Ganglion ciliare und der Pupillarreaction. Arch. f. Ophthmol. (Graefe's), Bd. 43.

BESTA, C. 1904 Richerche int. al modo cui si. stab. i rapp. mutui tra gli elementi nerv. embr. e sulla form. del retic. int. della cellula nerv. Riv. sper. di fren., tom. 30.

BETHE, A. 1903 Allgemeine Anatomie und Physiologie des Nervensystems. Leipzig.
1904 Der heutige Stand der Neuronlehre. Deutsch. Med. Wochenschr., Bd. 33.
1906 Bemerkungen zur Zellkettentheorie. Anat. Anz., Bd. 28.
1907 Neue Versuche über die Regeneration der Nervenfasern. Pflüger's Archiv, Bd. 116.

BIDDER, F., UND VON KUPFFER, C. 1857 Untersuchungen ueber das Ruckenmark. Leipzig.

Digitized by Google

Boeke, J. 1904 Beiträge zur Entwickelungsgeschichte der Teleostier. 2. Die Segmentirung des Kopfmesoderms, die Genese der Kopfhöhlen, das Mesectoderm der Ganglienleisten und die Entwickelung der Hypophyse bei den Muränoiden. Petrus Camper, Bd. 3.

Bonsdorff, E. J. 1852 Symbolae ad anatomiam comparatam nervorum animalium vertebratorum. I. Nervi cerebrales corvi cornicis. 2. Nervi cerebrales Gruis cinereae. Acta soc. sci. Fennicae, Bd. 3.

Boveri, Th. 1885 Beiträge zur Kenntnis der Nervenfasern. Abh. phys.-math. Kl. d. Acad. Wiss. München, Bd. 15.

Brachet, M. A. 1905 Sur l'histogenese et la signification morphol. des fibres nerveuses peripheriques. Bull. Soc. roy. sci. med. et nat. Bruxelles.
1907 Recherches sur l'ontogenese de la tete chez les amphibiens. Arch. de Biol., tom. 23.

Brauer, A. 1904 Beiträge zur Kenntniss der Entwicklung und Anatomie der Gymniophionen. IV. Die Entwickelung der beiden Trigeminus-Ganglien. Zool. Jahrb., Suppl. 7.

Braus, H. 1899 Beiträge zur Entwickelung der Muskulatur und des peripheren Nervensystems der Selachier. 1. Teil. Die metotischen Urwirbel und spinooccipitalen Nerven. Morph. Jahrb., Bd. 27.
1905 Experimentelle Beiträge zur Frage nach der Entwickelung peripherer Nerven. Anat. Anz., Bd. 26.

Brock, G. 1906 Untersuchungen über die Entwicklung der Neurofibrillen des Schweine-foetus. Monatschr. f. Psych. u. Neurol., Bd. 18.

Brodman, K. 1907 Bemerkungen über die Fibrillogenie und ihre Beziehungen zur Myelogenie mit besondrer Berücksichtigung des Cortex cerebri. Neurol. Centralbl.

Brohmer, P. 1909 Der Kopf eines Embryos von Chlamydoselachus und die Segmentirung des Selachierkopfes. Jen. Zeit. f. Naturwiss., Bd. 44.

Broman, I. 1895 Beschreibung eines menschlichen Embryos von beinahe drei mm. Lange mit spezieller Bemerkung über die bei demselben befindlichen Hirnfalten. Morph. Arbeiten., Bd. 5.

Budge, J. 1855 Ueber die Bewegung der Iris.

Burckhardt, R. 1892 Das Centralnervensystem von Protopterus annectans. Eine vergleichende anatomische Studie. Berlin.

Burrows, M. T. 1911 The growth of tissues of the chick embryo outside the animal body, with special reference to the nervous system. Jour. Exp. Zoöl., vol. 10.

Cajal, Ramón y, S. 1894 Les nouvelles idees sur la structure du système nerveux chez l'homme et chez les vertébrès. Rev. gen. sci. pures et appliqués, tom. 5.
1906 Genesis de la fibros nerviosos del embryon, observaciones contr. a la teoria catenaria. Trab. labor. inv. biol. Univ. Madrid, tom. 4.
1907 a Die histogenetischen Beweise der Neuronentheorie von His und Forel. Anat. Anz., 30.
1907 b Nouvelles observations sur l'évolution des neuroblasts avec quelques remarques sur l'hypothese neurogenique de Hensen-Held. Trav. d. lab. de rech. biol., Bd. 5. Also 1908, Anat. Anz., Bd. 22.

Digitized by Google

CAPOBIANCO, F. 1900 Della prima genesi delle cellule nervose della midolla e dei gangli spinali. Verhandl. Anat. Gesellsch., tom. 14. Pavia.
1902 Lo svilluppo della cellule nervose midollo spinnale di pollo. Annali di Neurologia, tom. 20.
1905 Rich. ulterieures sur la genese des cellules nerveux. Ann. di Neurol., tom. 23.

CAPOBIANCO, F., E FRAGNITO, O. 1898 Nuove richerche su la genesi e i rapporti mutui degli elementi nervosi e nervoglici. Ann. neurol., Milano, tom. 2–3.

CARPENTER, F. W. 1906 The development of the oculomotor nerve, the ciliary ganglion, and the abducent nerve in the chick. Bull. Mus. Comp. Zool. Harv. Coll., vol. 48.

CARPENTER, F. W., AND MAIN, R. C. 1907 The migration of medullary cells into the ventral nerve-roots of pig-embryos. Anat. Anz., Bd. 31.

CHIARUGI, G. 1891 Sur les myotomes et sur les nerfs de la tete posterièure et de la region proximale du tronc dans les embryons des amphibies anoures (résumé). Arch. Ital. de Biol., tom. 15.
1894 Lo sviluppo dei nervi oculomotore e trigemello. Nota preliminare. Monit. zool. ital., tom. 5.

COGGI, A. 1895 Il cordone gangliare anteriore in Torpedo e Pristiurus. Richerche fati nel labor. Anat. Univ. Roma ed in altri labor. biolog., tom. 5.

COGHILL, G. E. 1913 The primary ventral roots and somatic motor column of Amblystoma. Jour. Comp. Neur., vol. 23.

COLE, F. J. 1898 Reflections on the cranial nerves and sense organs of fishes. Trans. Liverpool Biol. Soc., vol. 12.

CORNING, H. K. 1899 Ueber die Entwickelung der Kopf- und Extremitatenmuskulatur bei Reptilien. Morph. Jahrb., Bd. 28.
1900 Ueber die vergleichende Anatomie der Augenmuskulatur. Morph. Jahrb., Bd. 29.

DEAN, B. 1899 On the embryology of Bdellostoma stouti. Festschr. zum 70-ten Geburtstag von C. von Kupffer.

DELSMAN, H. C. 1913 a Der Ursprung der Vertebraten. Zool., Anz., Bd. 41.
1913 b Ist das Hirnbläschen das Amphioxus dem Gehirn der Kranioten homolog? Anat. Anz., Bd. 44.

D'ERCHIA, F. 1894 Contributo allo studio della struttura e delle connessioni del ganglio ciliare. I. Sulla struttura del ganglio ciliare. Monit. zool. Ital., tom. 5.
1895 Contributo allo studio della struttura e delle connessioni del ganglio ciliare. II. Connessioni del ganglio ciliare. Monit. zool. Ital., tom. 6.

DIXON, A. F. 1895 On the development of the branches of the fifth cranial nerve in man (abstract). Proc. Roy. Soc. London, vol. 57.
1896 Full account of above paper. Trans. Roy. Soc. Dublin, vol. 6.

DOHRN, A. 1875 Der Ursprung der Wirbelthiere und das Princip des Functionswechsels. Genealogische Skizzen. Leipzig.
1885 Studien zur Urgeschichte des Wirbelthierkörpers. X. Zur Phylogenese des Wirbelthierauges. Mitt. Zool. Stat. Neapel, Bd. 6.

Digitized by Google

DOHRN, A. 1888 a Studien, u. s. w. 13. Ueber Nerven und Gefässe bei Ammocoetes und Petromyzon Planeri. Mitt. Zool. Stat. Neapel., Bd. 8.
1888 b Studien, u. s. w. 14. Ueber die erste Anlage und Entwicklung der motorischen Rückenmarksnerven bei den Selachiern., Bd. 8.
1890 a Bemerkungen über den neuesten Versuch einer Lösung des Wirbelthierkopf-Problems. Anat. Anz., Bd. 5.
1890 b Studien, u. s. w. 15. Neue Grundlagen zur Beurtheilung der Metamerie des Kopfes. Mitt. Zool. Stat. Neapel, Bd. 9.
1891 a Studien, u. s. w. 16. Ueber die erste Anlage und Entwicklung der Augenmuskelnerven bei Selachiern und das Einwandern von Medullarzellen in die motorischen Nerven. Mitt. Zool. Stat. Neapel., Bd. 10.
1891 b Studien u. s. w. 17. Nervenfaser und Ganglienzelle. Histogenetische Untersuchungen. Mitt. Zool. Stat. Neapel., Bd. 10.
1892 Die Schwann'schen Kerne der Selachierembryonen. Anat. Anz., Bd. 7.
1901 Studien, u. s. w. 18–21. Die Schwann'schen Kerne, ihre Herkunft und Bedeutung. Mitt. Zool. Stat. Neapel, Bd. 15.
1904 a Studien, u. s. w. 23. Die Mandibularhöhle der Selachier. Mitt. Zool. Stat. Neapel, Bd. 17.
1904 b Studien, u. s. w. 24 Die Praemandibularhöhle. Mitt. Zool. Stat. Neapel, Bd. 17.
1907 Studien, u. s. w. 25. Der Trochlearis. Mitt. Zool. Stat. Neapel, Bd. 18.

DUNN, ELIZABETH H. 1902 On the number and relation between diameter and distribution of the nerve fibers innervating the leg of the frog. Jour. Comp. Neur., vol. 12.

EDGEWORTH, F. H. 1907 The development of the head muscles in Gallus domesticus, and the morphology of the head muscles in the sauropsida. Quart. Journ. Micr. Sci., vol. 51.

EDINGER, L. 1896 Vorlesungen ueber den Bau der nervösen Centralorgane des Menschen und der Thiere. Leipzig.

EMMERT, J. 1900 Beiträge zur Entwickelungsgeschichte der Selachier, insbesondere nach Untersuchungen an jungeren Embryonen von Torpedo marmorata. Arch. f. mikr. Anat., Bd. 56.

EWART, J. C. 1890 On the development of the ciliary or motoroculi ganglion. Proc. Roy. Soc. London, vol. 47.

EYCLESHYMER, A. C. 1895 The early development of Amblystoma, with observations on some other vertebrates. Jour. Morph., vol. 10.

FILATOFF, D. 1907 Die Metamerie des Kopfes von Emys lutaria. Zur Frage über die korrelative Entwicklung. Morph. Jahrb., Bd. 38.

FRAGNITO, O. 1899 La cellula nervosa rappresenta un'unita embry.? Congr. della Soc. ital. fren. Napoli.

FRITZ, K. W. 1899 Untersuchungen über das Ganglion ciliare. Diss. Marburg.

FRORIEP, A. 1885 a Zur Entwickelungsgeschichte der Kopfnerven. Verh. Anat Ges. Munchen.
1885 b Ueber Anlagen von Sinnesorganen am Facialis, Glossopharyngeus und Vagus, über die genetische Stellung des Vagus zum Hypoglossus, und über die Herkunft der Zungenmuskulatur. Arch. Anat. u. Physiol., Anat. Abth.

Digitized by Google

FRORIEP, A. 1891 Zur Entwickelungsgeschichte der Kopfnerven. Verh. Anat. Gesellsch. Munchen.

1892 a Entwickelungsgeschichte des Kopfes. Ergebnisse Anat. u. Entw'g., Bd. 1.

1892 b Zur Frage der sogenannten Neuromerie. Verhdl. Anat. Gesellsch. Wien.

1894 Entwickelungsgeschichte des Kopfes. Ergeb. Anat. u. Entwickl., Bd. 3.

1901 Ueber die Ganglienleisten des Kopfes und des Rumpfes und ihre Kreutzung in der Occipitalregion. Arch. f. Anat. u. Physiol., Anat. Abth.

1902 a Zur Entwickelungsgeschichte des Wirbelthierkopfes. Verhandl. Anat, Gesellsch. Halle.

1902 b Einige Bemerkungen zur Kopffrage. Anat. Anz., Bd. 21.

1907 Ueber Entwicklung und Bau des autonomen Nervensystems. Med. naturwiss. Archiv, Bd. 1.

1908 Ueber die elemente des peripherischen Nervensystems und ihre Entwickelung, in Edinger's Vorlesungen über den Bau der nervösen Centralorgane, Bd. 2, Leipzig.

FÜRBRINGER, M. 1897 Ueber die spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie. Festschr. zum 70-ten Geburtstag. von Carl Gegenbaur, Bd. 3.

1902 Morphologische Streitfragen. 1. Nervus trochlearis. 2. Rabl's Methode und Behandlung der Extremitaten-frage. Morph. Jahrb., Bd. 30.

FUSARI, R. 1890 Contribution à l'étudé du développement des capsules surrenales et du sympathetique chez le poulet et chez les mammifères. Archivio per le scienze mediche, tom. 16.

GASKELL, W. H. 1899 On the relation between the structure, function, distribution and origin of the cranial nerves; together with a theory of the origin of the nervous system of Vertebrata. Jour. Physiol., vol. 10.

GAST, R. 1909 Die Entwickelung des Oculomotorius und seiner Ganglien bei Selachierembryonen. Mitt. Zool. Stat. Neapel, Bd. 19.

GEGENBAUR, C. 1871 Ueber die Kopfnerven von Hexanchus. Jen. Zeitschr. Natwiss., Bd. 6.

1872 Untersuchungen zur vergleichenden Anatomie der Wirbelthiere. 3. Das Kopfskelett der Selachier. Ein Beitrag zur Erkenntniss der Genese des Kopfskelettes der Wirbelthiere. Leipzig.

1887 Die Metamerie des Kopfes und die Wirbeltheorie des Kopfskelettes. Morph. Jahrb., Bd. 13.

1898 Vergleichende Anatomie der Wirbelthiere mit Berücksichtigung der Wirbellosen. Leipzig.

GIERLICH, N. 1906 Ueber die Entwickelung der Neurofibrillen in der Pyramidenbahn des Menschen. Neurol. Centralbl.

1907 a Kurze Bemerkungen über Fibrillogenie im Zentralnervensystem des Menschen zur Arbeit Brodmann's 'Bemerkungen über die fibrillogenie und ihre Beziehungen zur Myelogenie mit besonderer Berücksichtigung des Cortex cerebri.' Neurol. Centralbl.

Digitized by Google

GIERLICH, N. 1907 b Ueber das verschiedene Verhalten der Neurofibrillen in den Fortsätzen und im Zelleib der motorischen Ganglienzellen. Neurol. Centralbl.

GIERLICH, N., UND HERZHEIMER, G. 1907 Studien über Neurofibrillen im Zentralnervensystem. Wiesbaden.

GIGLIO-TOS, E. 1902 Sulla cellule germinative del tubo midollare embryonale dell'uomo. Anat. Anz., Bd. 20.

GOETTE, A. 1875 Die Entwickelungsgeschichte der Unke (Bombinator igneus) als Grundlage eine vergleichenden Morphologie der Wirbelthiere. Leipzig.

1888 Ueber die Entwicklung von Petromyzon fluviatilis. Zool. Anz., Bd. 11.

1890 Entwickelungsgeschichte des Flussneunauges (Petromyzon fluviatilis). Hamburg und Leipzig.

GOLDBERG, M. 1891 Ueber die Entwickelung der Ganglien beim Hühnchen. Arch. f. Mikr. Anat., Bd. 37.

GOLGI, C. 1893 Intorno all'origine del quarto cerebralo (patetico o trocleare) e di una questione di isto-fisiologia generale che a questa argumentosi collega. Atti Accad. Lincei, Rendiconti, tom. 2. Also in French; Arch. Ital. Biol., tom. 19.

GOLOWINE, E. 1890 Sur le développement du système ganglionnaire chez le poulet. Anat. Anz., Bd. 5.

GORONOWITSCH, N. 1888 Das Gehirn und die Cranialnerven von Acipenser ruthenus. Ein Beitrag zur Morphologie des Wirbelthierkopfes. Morph. Jahrb., Bd. 13.

1892 Die axiale und die laterale (A. Goette) Kopfmetamerien der Vogelembryonen. Die Rolle der sog. Ganglienleisten im Aufbaue der Nervenstamme. Anat. Anz., 7.

1898 Untersuchungen über die erste Anlage der Cranialnerven bei Salmo fario. Nouveaux Mem. Soc. Imp. Natural. Moscou, Bd. 16.

GRÄPER, L. 1913 Die Rhombomeren und ihre Nervenberichungen. Arch. mikr. Anat. Bd. 83.

GRIGGS, L. 1910 Early stages in the development of the central nervous system of Amblystoma punctatum. Jour. Morph., vol. 21.

GURWITSCH, A. 1900 Die Histogenese der Schwann'schen Scheide. Arch. f. Anat. u. Physiol., Anat. Abth.

GUTHKE, E. 1906 Embryologische Studien über die Ganglien und Nerven des Kopfes von Torpedo ocellata. Jen. Zeitschr., Bd. 42.

HALLER, B. 1898 Vom Bau des Wirbelthiergehirns. I Theil. Salmo und Scyllium. Morph Jahrb., Bd. 26.

HARRISON, R. G. 1901 a The histogenesis of the peripheral nervous system in Salmo salar. Biol. Bull., vol. 2.

1901 b Ueber die Histogenese des peripheren Nervensystems bei Salmo salar. Arch. mikr. Anat., Bd. 57.

1904 Neue Versuche und Beobachtungen über die Entwickelung der peripheren Nerven der Wirbeltiere. Stizungsber. Niederrhein. Ges. Bonn.

Digitized by Google

HARRISON, R. G. 1906 Further experiments on the development of peripheral nerves. Am. Jour. Anat., vol. 5.

1907 a Experiments in transplanting limbs and their bearing upon the problems of the development of nerves. Jour. Exp. Zoöl., vol. 4.

1907 b Observations upon the living developing nerve fiber. Amer. Jour. Anat., vol. 7.

1910 The development of peripheral nerve fibers in altered surroundings. Arch. f. Entwickelungsmech. d. Organismen., Bd. 30.

1911 The outgrowth of the nerve fiber as a mode of protoplasmic movement. Jour. Exp. Zoöl., vol. 9.

HATSCHEK, B. 1881 Studien über Entwicklung des Amphioxus. Arb. Zool. Inst. Wien, Bd. 4.

1892 Die Metamerie des Amphioxus und des Ammocoetes. Verh. Anat. Gesellsch., Wien.

1893 Zur Metamerie der Wirbelthiere. Anat. Anz., Bd. 8.

HELD, H. 1897 Beiträge zur Structur der Nervenzellen und ihre Fortsätze. Arch. f. Anat. u. Physiol., Anat. Abth.

1904 Zur weiteren Kenntniss der Nerven, u. s. w. Abh. d. Kgl. sachs. Ges. d. W., Bd. 29.

1906 Zur Histogenese der Nervenleitung. Verh. Anat. Ges., Rostock.

1907 a Kritische Bemerkungen zu der Verteidigung der Neuroblasten- und Neuronenlehre durch R. Cajal. Anat. Anz.

1907 b Ueber den Begriff der Wirbeltierganglienzelle. Verh. der. Ges deutsch. Naturf. und Aerzte, Dresden.

1907 c Zur Kenntnis der marg. Neuroglia. Verh. d. Ges. deutsch. Naturf. u. Aerzte, Dresden.

1909 Die Entwicklung des Nervengewebes bei den Wirbeltieren. Leipzig.

HENSEN, V. 1864 Zur Entwickelung des Nervensystems. Arch. f. path. Anat. u. Physiol., Bd. 30.

1876 Beobachtungen über die Befruchtung und Entwicklung des Kaninchens und des Meerschweinschens. Zeit. Anat. u. Entwickl., Bd. 1.

1903 Die Entwicklungsmechanik der Nervenbahnen im Embryo der Saugethiere. Kiel u. Leipzig.

1908 Ueber das Auswachsen der Nerven im Embryo. München. Med. Woch., Bd. 55.

HENSEN, V., UND VÖLKERS, C. 1868 Experimentaluntersuchungen über den Mechanismus der Accommodation. Kiel.

HERMS, E. 1884 Ueber die Bildungsweise der Ganglienzellen im Ursprungsgebiete des Nervus acustico-facialis bei Ammocoetes. Sitzb. München. Akad., Math.-phys. Cl., Bd. 14.

HERRICK, C. J. 1899 The cranial and first spinal nerves of Menidia: A contribution upon the nerve components of the bony fishes. Jour. Comp. Neur., vol. 9.

1903 The doctrine of nerve components and some of its applications. Jour. Comp. Neur., vol. 13.

Digitized by Google

HERRICK, C. J. 1909 The criteria of homology in the peripheral nervous system. Jour. Comp. Neur., vol. 19.

HERRICK, C. L. 1892 Embryological notes on the brain of the snake. Jour. Comp. Neur., vol. 2.

1893 The development of medullated nerve-fibers. Jour. Comp. Neur., vol. 3.

HERTWIG, O. UND R. 1878 Das Nervensystem und die Sinnesorgane der Medusen, Monographisch dargestellt. Leipzig.

HEYMANS, J. F., UND VAN DER STRICHT, O. 1898 Sur le système nerveux de l'Amphioxus et en particulier sur la constitution et la génese des racines sensibles. Mem. cour. par. l, Acad. Roy. Sci. Belgium, Bd. 56.

HIS, W. 1879 Ueber die Anfänge des peripherischen Nervensystems. Arch. f. Anat. u. Physiol., Anat. Abth.

1888 a Die Entwickelung des ersten Nervenbahnen beim menschlichen Embryo. Uebersichtliche Darstellung. Arch. f. Anat. Physiol., Anat. Abth., Bd. 6.

1888 b Die morphologische Betrachtung der Kopfnerven. Eine kritische Studie. Arch. f. Anat. u. Physiol., Anat. Abth., Bd. 6.

1888 c Zur Geschichte des Gehirns, sowie der centralen und peripherischen Nervenbahnen beim menschlichen Embryo. Abh. sachs. Gesellsch. Wissensch., Math.-phys. Cl. Bd. 4.

1889 Die Neuroblasten und deren Entstehung im embryonalen Mark. Abh. sachs. Gesell. Wiss. Leipzig., Math.-phys. Cl., Bd. 15. Also in Arch. f. Anat. u. Physiol., Anat. Abth.

1890 Histogenese und Zusammenhang der Nervenelemente. Arch. Anat. u. Physiol., Anat. Abth., Suppl.

HIS, JR., W. 1897 Ueber die Entwickelung des Bauchsympathicus beim Hünchen und Menschen. Arch. Anat. u. Physiol., Anat. Abth., Suppl.

HIS, JR., W., AND ROMBERG, E. 1890 Beiträge zur Hirninnervation. Fortschr. d. Medicin., Bd. 8.

1891 Die Entwickelung des Herznervensystems bei Wirbelthieren. Abhandl. Math.-Phys. Classe König. sachs. Gesellsch. Wiss., Bd. 28.

HOFFMAN, C. K. 1885 Weitere Untersuchungen zur Entwicklungsgeschichte der Reptilien. Morph. Jahrb., Bd. 11.

1889 Ueber die Metamerie des Nachhirns und Hinterhirns, und ihre Beziehung zu den segmentalen Kopfnerven bei Reptilienembryonen. Zool. Anz., Bd. 12.

1894 Zur Entwickelungsgeschichte des Selachierkopfes. Anat. Anz., Bd. 9.

1896 Beiträge zur Entwickelungsgeschichte der Selachii. Morph. Jahrb., Bd. 24.

1897 Beiträge zur Entwickelungsgeschichte der Selachii. Morph. Jahrb., Bd. 25.

1899 Beiträge zur Entwickelungsgeschichte der Selachii. Morph. Jahrb., Bd. 27.

1900 Zur Entwickelungsgeschichte des Sympathicus. Die Entwickl. des Sympathicus bei den Selachiern. Verh. Akad. Amsterdam, Bd. 7.

Digitized by Google

HOFFMAN, C. K. 1902 Zur Entwickl. des Sympathicus. II. Die Entwicklung des Sympathicus bei den Urodelen. Verhdl. d. Konigl.. Akad. v. Wetensch. te Amsterdam, Bd. 8.

HOLTZMANN, H. 1896 Untersuchungen über Ciliarganglion und Ciliarnerven. Morph. Arbeit., Bd. 6.

HOUSER, G. L. 1901 The neurones and the supporting elements of the brain of a selachian. Jour. Comp. Neur., vol. 11.

HOUSSAY, F. 1890 Études d'embryologie sur les Vértebrès. Archiv de Zool. exp. et gen., tom. 8.

HUBER, G. C. 1897 Lectures on the sympathetic nervous system. Jour. Comp. Neur., vol. 7.

1899 A contribution on the minute anatomy of the sympathetic ganglia of the different classes of vertebrates. Jour. Morph., vol. 16.

HUXLEY, T. H. 1858 The Croonian lecture: On the theory of the vertebrate skull. Proc. Roy. Soc. London., vol. 9.

JEGOROW, J. 1886–1887 Recherches anatomo-physiologiques sur le ganglion ophthalmique. Archiv slav. biol., tom. 2, 3.

JOHNSON, ALICE, AND SHELDON, LILLIAN 1886 On the development of the cranial nerves of the newt. Proc. Roy. Soc. London, vol. 40.

JOHNSON, C. E. 1913 The development of the prootic head somites and eye muscles in Chelydra serpentina. Amer. Jour. Anat., vol. 14.

JOHNSTON, J. B. 1902 a An attempt to define the primitive functional divisions of the central nervous system. Jour. Comp. Neur., vol. 12.

1902 b Das Gehirn und die Cranialnerven der Anamnier. Ergebnis. d. Anat. u. Entwg., Bd. 11.

1905 a The morphology of the vertebrate head from the viewpoint of the functional divisions of the nervous system. Jour. Comp. Neur., vol. 15.

1905 b The cranial nerve components of Petromyzon. Morph. Jahrb., Bd. 34.

1906 The nervous system of vertebrates. Philadelphia.

1908 Additional notes on the cranial nerves of Petromyzonts. Jour. Comp. Neur., vol. 18.

1909 The morphology of the forebrain vesicle in vertebrates. Jour. Comp. Neur., vol. 19.

JONES, W. C. 1905 Notes on the development of the sympathetic nervous system in the common toad. Jour. Comp. Neur., vol. 15.

JORIS, H. 1904 Histogenese du neurone. Bull. de l'acad. royale de Med. de Belgique.

JULIN, CH. 1887 Le système nerveux grand sympathètique de l'ammocoetes (Petromyzon pl.). Anat. Anz., Bd. 2.

KALLIUS, E. 1900 Ergebniss. Ergeb. d. Anat. u. Entwckl., Bd. 9.

KAPPERS, C. U. A. 1904 Recherches sur le développement des gaines dans le tube nerveux. Petrus Camper, tom. 2.

1910 The migrations of the abducens nucleus and the concomitating changes of its root-fibers. Psych. en Neurol. Bladen, Bd. 4.

KASTSCHENKO, N. 1888 Zur Entwicklungsgeschichte des Selachierembryos. Anat. Anz., Bd. 3.

Digitized by Google

KERR, GRAHAM J. 1902 The early development of muscles and motor nerves in Lepidosiren. Rep. Brit. Assoc. Adv. Sci., Belfast.

1903 The development of Lepidosiren paradoxa. 3. Development of the skin and its derivatives. Quart. Jour. Micr. Sci., vol. 46.

1904 On some points in the early development of motor nerve trunks and myotomes in Lepidosiren paradoxa (Fitz.). Trans. R. Soc., Edinburgh, vol. 41.

1910 The development of the peripheral nerves of vertebrates. Presidential address. Proc. Roy. Soc. Phys., Edinburgh, vol. 18.

KILLIAN, G. 1891 Zur Metamerie des Selachierkopfes. Verh. Anat. Gesell. München.

KINGSLEY, J. S. 1897 The segmentation of the head. Biol. Lect., Marine Biol. Lab., Woods Hole, 1895.

1912 Comparative anatomy of vertebrates. Philadelphia.

KLINKHARDT, W. 1905 Beiträge zur Entwickelungsgeschichte der Kopfganglien und Sinneslinien bei Selachiern. Jena. Zeit. f. Naturwiss., Bd. 40.

VON KÖLLIKER, A. 1879 Entwicklungsgeschichte des Menschen und der höheren Thiere. Leipzig.

1885 Histologische Studien an Batrachierlarven. Zeit. wiss. Zool., Bd. 43.

1892 Ueber die Entwickelung der Elements des Nervensystems, contra Beard und Dohrn. Anat. Anz., Bd. 7, Ergänzungsh.

1894 a Ueber die feinere Anatomie und die physiologische Bedeutung des sympathischen Nervensystems. Verh. Gesell. deutsch. Naturf. u. Aerz, Versam, Bd. 1.

1894 b Ueber das Vorkommen von Nervenzellen in den vorderen Würzeln der Rückenmarksnerven der Katze. Verh. Gesel. deutsch. Naturf. u. Aerz., Bd. 2.

1896 Handbuch der Gewerbelehre des Menschen. Leipzig.

1900 Gegen die Entstehung von Nervenfasern aus Zellenstrangen. Anat. Anz., Bd. 18.

1905 Die Entwickelung der Elemente des Nervensystems. Zeitschr. f. wiss. Zool., Bd. 82.

KOHN, A. 1905 Ueber die Entwickelung des peripheren Nervensystems. Verh. Anat. Ges., Jena.

1906 Ganglienzelle und Nervenfaser. Münch. med. Wochenschr.

1907 Ueber die Entwickelung des sympathischen Nervensystems der Säugethiere. Arch. f. mikr. Anat., Bd. 70.

KOLSTER, R. 1899 Beiträge zur Kenntniss der Histogenese der peripheren Nerven nebst Bemerkungen über die Regeneration derselben nach Vorletzungen. Beitr. z. path. Anat., Bd. 26.

KOLTZOFF, N. K. 1901 Entwicklungsgeschichte des Kopfes von Petromyzon planeri. Ein Beitrag zur Lehre über Metamerie des Wirbeltierkopfes. Bull. Soc. Nat. Moscou, Bd., 15; German trans. 1902.

KRAUSE, W. 1881 Ueber die Doppelnatur des Ganglion ciliare. Morph. Jahrb., Bd. 7.

KUHL, H. UND VON HASSELT. 1820 Beitrag zur Kenntnis des Kopfes der Knorpelfische. Kuhl's Beitr. z. Zool. u. vergl. Anat. Bd. 2.

Digitized by Google

KUNTZ, A. 1910 The development of the sympathetic nervous system in mammals. Jour. Comp. Neur., vol. 20.

1911 The development of the sympathetic nervous system in certain fishes. Jour. Comp. Neur., vol. 21.

VON KUPFFER, C. 1885 Primäre Metamerie des Neuralrohrs der Vertebraten. Sitzungsber. Math. physik. Kl. München.

1890 Die Entwickelung von Petromyzon planeri. Arch. f. mikr. Anat., Bd. 35.

1891 Die Entwickelung der Kopfnerven der Vertebraten. Verh. Anat. Gesell. München.

1894 Studien zur vergleichenden Entwickelungsgeschichte des Kopfes der Kranioten. 2. Die Entwicklung des Kopfes von Ammocoetes planeri. München und Leipzig.

1895 Studien zur vergleichenden Entwicklungsgeschichte u. s. w. 3. Die Entwicklung der Kopfnerven von Ammocoetes planeri. München und Leipzig.

1906 Die Morphogenie des Centralnervensystems. Handbuch vergl. u. exp. Entwicklungslehre d. Wirbelthiere, Bd. 2.

LAMB, A. B. 1902 The development of the eye muscles in Acanthias. Am. Jour. Anat., vol. 1. Reprint in Tufts Coll. Stud., no. 7.

LANGENDORFF, O. 1894 Ciliarganglion und Oculomotorius. Arch. f. ges. Physiol., Bd. 56.

LANGLEY, J. N., AND ANDERSON, H. K. 1892 The action of nicotin on the ciliary ganglion and on the endings of the third cranial nerve. Jour. Physiol., vol. 13.

LEGROS, R. 1898 Développement de la cavitè buccale de l'Amphioxus lanceolatus. Contribution à l'étude de la morphologie de la tête. Arch. Anat. Micr., tom. 1 et 2.

VON LENHOSSEK, M. 1890 Ueber Nervenfasern in den hinteren Würzeln, welche aus dem Vorderhorn entspringen. Anat. Anz., Bd. 5.

1891 Zur Kenntnis der ersten Entstehung der Nervenzellen und Nervenfasern beim Vogelembryo. Verh. 10 Inter. med. Kong., Bd. 2.

1892 Beobachtungen an den Spinalganglien und dem Rückenmark von Pristiurusembryonen. Anat. Anz., Bd. 7.

1897 Nervensystem. Ergeb. Anat. u. Entwickl., Bd. 7.

1906 Frage nach der Entwickelung der peripherischen Nervenfasern. Anat. Anz., Bd. 28.

LEWIS, W. H. 1906 Experimental evidence in support of the outgrowth theory of the axis cylinder. Proc. Am. Ass. Anat., Ann Arbor, 1905. Am. Jour. Anat., vol. 5.

1907 Experimental evidence in support of the theory of outgrowth of the axis cylinder. Amer. Jour. Anat., vol. 6.

LILLIE, F. R. 1908 The development of the chick. New York.

LOCY, W. A. 1895 Contribution to the structure and development of the vertebrate head. Jour. Morph., 11.

1904 A new cranial nerve in selachians. Mark Anniv. Vol.

LONDON UND PESKER 1906 Ueber die Entwicklung des peripheren Nervensystems bei Säugetieren (weissen Mäusen). Arch. f. mikr. Anat., Bd. 67.

Digitized by Google

MARCUS, H. 1909 Ueber den Sympathicus. Sitzungsber. Gesell. Morph. u. Physiol. München.

MARINA, A. 1898 Il neurone del ganglio ciliare ed i centri dei movimenti pupillare. Riv. di patolog. nerv. e ment., tom. 3.

1899 Das Neuron des Ganglionciliare und die Centra der Pupillenbewegungen. Eine experimentelle Studie. Deutsch. Zeitschr. f. Nervenheilk., Bd. 14.

MARSHALL, A. M. 1878 The development of the cranial nerves of the chick. Quart. Jour. Micr. Sci., vol. 18.

1881 On the head cavities and associated nerves of elasmobranchs. Quart. Jour. Micr. Sci., vol. 21.

1882 The segmental value of the cranial nerves. Jour. Anat. Physiol., vol. 16. Also, Stud. Biol. Lab. Owens Coll., vol. 1, 1886.

MARSHALL, A. M., AND SPENCER, W. B. 1881 Observations on the cranial nerves of Scyllium. Quart. Jour. Micr. Sci., vol. 21. Also in Stud. Biol. Lab. Owens Coll., vol. 1, 1886.

MARTIN, P. 1890 Die erste Entwickelung der Kopfnerven der Katze. Oesterr. Monatsschr. Thierheilkunde, Bd. 15.

1891 Die Entwickelung der neunten bis zwölften Kopfnerven bei der Katze. Anat. Anz., Bd. 6.

McCLURE, C. F. W. 1882 The primitive segmentation of the vertebrate brain. Zool. Anz., Bd. 12.

1890 The segmentation of the primitive vertebrate brain. Jour. Morph., vol. 4.

McMURRICH, J. PLAYFAIR 1912 The problem of the vertebrate head in the light of comparative anatomy. Proc. 7th Internat. Cong., Boston, 1907.

MEEK, A. 1909 The encephalomeres and cranial nerves of an embryo of Acanthias vulgaris. Anat. Anz., Bd. 34.

1910 The cranial segments and nerves of the rabbit with some remarks on the phylogeny of the nervous system. Anat. Anz., Bd. 36.

VON MIHALKOWITZ, V. 1877 Entwickelungsgeschichte des Gehirns. Leipzig.

VON MIKLUCHO-MACLAY, N. 1868 Beitrag zur vergleichenden Anatomie des Gehirns. Jenaische Zeitschr. f. Naturwiss., Bd. 4.

MINOT, C. S. 1892 Human embryology. New York.

1896 Die frühen Stadien und die Histogenese des Nervensystems. Ergeb. Anat. u. Entwickg., Bd. 6.

1897 Cephalic homologies. A contribution to the determination of the ancestry of vertebrates. Amer. Nat., vol. 31.

1910 Laboratory text-book of embryology. Philadelphia.

MITROPHANOW, P. 1892 Note sur la signification metamerique des nerfs craniens. Congrès Internat. Zool. Muscou, Bd. 1.

1893 Étude embryogenique sur les selachiens. Arch. Zool. Expér., tom. 1.

MONCKEBERG, G., UND BETHE, A. 1899 Die Degeneration der markhaltigen Nervenfasern der Wirbeltiere unter hauptsächlicher Berücksichtigung des Verhaltens der Primitiv-fibrillen. Arch. micr. Anat., Bd. 54.

NAWROCKI, F., UND PRZYBYLSKI, J. 1891 Die pupillenerweiternden Nerven der Katze. Arch. f. ges. Physiol., Bd. 50.

Digitized by Google

NEAL, H. V. 1896 A summary of studies of the segmentation of the nervous system of Squalus acanthias. Anat. Anz., Bd. 12.

1897 The development of the hypoglossus musculature in Petromyzon and Squalus. Anat. Anz., Bd. 13.

1898 a The segmentation of the nervous system in Squalus acanthias. A contribution to the morphology of the vertebrate head. Bull. Mus. Comp. Zool. Harvard Coll., vol. 31.

1898 b The problem of the vertebrate head. Jour. Comp. Neur., vol. 8.

1903 The development of ventral nerves in Selachii. I. Spinal ventral nerves. Mark Anniv. Vol.

1912 The morphology of the eye muscle nerves. Proc. 7th Internat. Cong., Boston, 1907; Separate pub. in 1909.

NEUMAYER, L. 1906 Histo- u. Morphogenese des peripheren Nervensystems der Spinalganglien und des Nervus sympathicus. Handbuch d. vergl. u. exp. Entwickelungslehre der Wirbeltiere, Bd. 2.

NICOLAS, A. 1900 Note sur la presence de fibres musculaires strias dans la gland pineale de quelques mammifères. Compt. Rend. Soc. Biol., tom. 52.

NORRIS, H. W. 1891 Recent studies of the vertebrate head. Amer. Nat., vol. 25.

ONODI, A. D. 1884 Ueber die Entwickelung der Spinalganglien und der Nervenwürzeln. Internat. Monatschr. f. Anat. u. Histol., Bd. 1.

1886 Über die Entwicklung des sympathischen Nervensystems. Arch. f. mikr. Anat., Bd. 26.

OPPEL, A. 1890 Ueber Vorderkopfsomiten und die Kopfhöhle bei Anguis fragilis. Arch. f. mikr. Anat., Bd. 36.

ORR, H. B. 1887 Contribution to the embryology of the lizard. Jour. Morph., vol. 1.

OSBORN, H. F. 1888 A contribution to the internal structure of the amphibian brain. Jour. Morph., vol. 2.

OSTROUMOFF, A. 1889 Regio occipitalis. Eine morphologische Studie. Arb. Naturf. Ges. an d. Univ. Kasan., Bd. 21.

PARKER, G. H. 1900 The neurone theory in the light of recent discoveries. Amer. Nat., vol. 34.

1908 The origin of the lateral eyes of vertebrates. Amer. Nat., vol. 42.

1910 The phylogenetic origin of the nervous system. Anat. Rec., vol. 4.

PATON, S. 1907 The reactions of the vertebrate embryo to stimulation and the associated changes in the nervous system. Mitt. Zool. Stat. Neapel, Bd. 18.

PATERSON, A. M. 1890 Development of the sympathetic nervous system in mammals. Phil. Trans. Roy. Soc., vol. 181.

1898 Preliminary note on the development of the sympathetic system in elasmobranchs. Brit. Med. Jour.

PATTEN, W. 1912 The evolution of the vertebrates and their kin. Philadelphia.

Digitized by Google

La Pegna, E. 1904 Su la genesi ed i rapp. recipr. de-gle elemente nervose nel midollo spinali di pollo. Ann. di Neurol., tom. 22.

1905 Sulla trasformazione delle radice spinale e sulla prima comparsa di fibrille nelle cellule del midollo. Riv. sper. di freniatria, tom. 31.

Pighini, G. 1904 Sulla sviluppo della fibre nervose periferichi e centrali spinali e ganglione cefalici nell'embrione dell pollo. Riv. sper. di freniatria, tom. 30.

1905 Sur l'origine et la formation des cellules nerveuses chez les embryons de selaciens. Bibl. anat., tom. 14.

Pinkus, F. 1894 Ueber einen noch nicht beschriebenen Hirnnerven des Protopterus annectans. Anat. Anz., Bd. 9.

Pitzorno, M. 1910 Sulla struttura dei gangli simpatici nei Selaci. Monit. Zool. Ital., tom. 21.

Platt, Julia B. 1890 The anterior head-cavities of Acanthias. Zool. Anz., Bd. 13.

1891 A contribution to the morphology of the vertebrate head, based on a study of Acanthias vulgaris. Jour. Morph., vol. 5.

1891 b Further contribution to the morphology of the vertebrate head. Anat. Anz., Bd. 6.

1896 Ontogenetic differentiations of the ectoderm in Necturus. 2. On the development of the peripheral nervous system. Quart. Jour. Micr. Sci., vol. 38.

1897 The development of the cartilaginous skull and of the branchial and hypoglossal musculature in Necturus. Morph. Jahrb., Bd. 25.

Pollard, H. B. 1891 On the anatomy and phylogenetic position of Polypterus. Zool. Jahrb., Bd. 5.

Prenant, A. 1889 Note sur l'existence des replis médullaires chez l'embryon du porc. Bull. Soc. Sci. Nancy, tom. 9.

Prentiss, C. W. 1904 The nervous structures in the palate of the frog; the peripheral networks and the nature of their cells and fibers. Jour. Comp. Neur., vol. 14.

Rabl, C. 1885 Bemerkung über die Segmentirung des Hirnes. Zool. Anz., Bd. 8.

1889 a Theorie des Mesoderms. Morph. Jahrb., Bd. 15.

1889 b Ueber die Prinzipien der Histologie. Verh. d. Anat. Gesellsch. Berlin.

1892 Ueber die Metamerie des Wirbeltierkopfes. Verh. Anat. Gesellsch. Wien.

1901 Gedanken und Studien über den Ursprung der Extremitäten. Zeit. f. wiss. Zool., Bd. 70.

Raffaele, F. 1900 Per la genese dei nervi da catene cellulari. Anat. Anz., Bd. 18.

Ransom, W. B., and Thompson, D'A. W. 1886 On the spinal and visceral nerves of cyclostomata. Zool. Anz., Bd. 9.

vom Rath, O. 1895 Zur Conservirungstechnik. Anat. Anz., Bd. 11.

Reighard, J. 1902 On the anterior head-cavity of the elasmobranchs. Rep. Mich. Acad. Sci., 1901.

Digitized by Google

REMAK, R. 1837 Weitere mikroskopische Beobachtungen über die Primitivfasern des Nervensystems der Wirbeltiere. Froriep's Notizen, Bd. 3.
1847 On the independent alimentary nervous system. Berlin.
1855 Untersuchungen über die Entwickelung der Wirbelthiere. Berlin.

RETZIUS, G. 1881 Untersuchungen über die Nervenzellen der cerebro-spinalen Ganglien und der übrigen peripherischen Kopfganglien mit besonderer Rücksicht auf die Zellenausläufer. Arch. f. Anat. u. Physiol., Anat. Abt.
1893 Zur Kenntnis der ersten Entwickelung der nervösen Elemente im Rückenmark des Hünchens. Biol. Unters., Bd. 5.
1894 Ueber das Ganglion ciliare. Anat. Anz., Bd. 9.

REUTER, K. 1897 Ueber die Entwickelung der Augenmuskulatur beim Schwein Anat. Hefte, Bd. 9.

REX, H. 1897 Ueber das Mesoderm des Vorderkopfes der Ente. Arch. f. mikr. Anat., Bd. 50.
1900 Zur Entwicklung der Augenmuskulatur der Ente. Archiv für mikr. Anat., Bd. 57.
1905 Ueber d. Mesoderm der Vorderkopfes d. Lachmöse. Morph. Jahrb., Bd. 33.

ROHON, V. 1884 Zur Histiologie des Rückenmarks der Forelle. Sitz. Ber. Akad. Wiss. München, Bd. 1.

SAGEMEHL, M. Untersuchungen über die Entwickelung der Spinalnerven (Diss.) Dorpat.

SCHAEPPE, TH. 1904 Ueber den Zusammenhang von Muskel und Nerv bei den Siphonophoren. Ein Beitrag zur Neuromuskeltheorie. Mitth. d. Naturwiss. Ges. Winterthur.
1909 Kritische Bemerkungen zur Frage nach der Entstehung der Nerven. Anat. Anz., Bd. 35.

SCAMMON, R. E. 1911 Normal plates on the development of Squalus acanthias. Normentafeln zur Entwicklungsgeschichte der Wirbelthiere, herausgegeben von F. Keibel.

SCHLACHER, A. 1801 De cataracta.

SCHAFER, A. E. 1881 Note on the occurrence of ganglion cells in the anterior roots of the cat's spinal nerves. Proc. Roy. Soc. London, vol. 31.

SCHAPER, A. 1894 Die morphologische und histologische Entwicklung des Kleinhirns der Teleostier. Morph. Jahrb., Bd. 21.
1897 Die frühesten Differenzirungsvorgänge im Centralnervensystem. Kritische Studie und Versuch einer Geschichte der Entwickelung nervöser Substanz. Arch. f. Entwickl. Mech., Bd. 5.

SCHENCK, S., UND BIRDSALL, W. R. 1878 Ueber die Lehre von der Entwickelung der Ganglien des Sympathicus. Mitt. aus d. embryol. Inst. Wien., Bd. 3.

SCHIEFFERDECKER, P. 1906 Neurone und Neuronenbahnen. Leipzig.

SCHNEIDER, A. 1879 Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte der Wirbelthiere. Berlin.
1880 Ueber die Nerven von Amphioxus, Ammocoetes, und Petromyzon. Zool. Anz., Bd. 3.

Digitized by Google

SCHULTZE, O. 1904 a Ueber die Entwickelung des peripheren Nervensystems Verh. Anat. Ges., Bd. 18. Vers.

1904 b Nachtrag zu meinem auf der Anatomenversammlung in Jena gehaltenen Vortrag ueber die Entwickelung des peripheren Nervensystems. Anat. Anz., Bd. 25.

1905 a Beiträge zur Histogenese des Nervensystems. 1. Ueber die multizellulare Entstehung des peripheren sensiblen Nervenfaser, u. s. w., Arch. f. mikr. Anat., Bd. 66.

1905 b Die Continuität der Organisationseinheiten der peripheren Nervenfäser. Pflüger's Archiv, Bd. 108.

1905 c Weiteres zur Entwicklung der peripheren nerven, u. s. w. Verhandl. d. phys.-med. Ges. zu Würzburg, Bd. 37.

1906 Zur Histogenese der peripheren Nerven. Verh. d. anat. Gesell. Rostock.

1908 Zur Histogenese des Nervensystems. Sitzungsber. d. kgl. pr. Ak. d. Wiss., Bd. 6.

SCHWALBE, G. 1879 a Das Ganglion oculomotorii. Ein Beitrag zur vergleich. Anatomie der Kopfnerven. Jena. Zeitschr., Bd. 13.

1879 b Ueber die morphologische Bedeutung des Ganglion ciliare. Sitzungsber. Jena. Gesell. f. med. u. Naturwiss., 1878.

1881 Lehrbuch der Histologie. Erlangen.

SCHWANN, TH. 1839 Mikroskopische Untersuchungen über die Uebereinstimmung in der Structur und dem Wachstum der Thiere und Pflanzen. Berlin.

SCOTT, W. B. 1887 Notes on the development of Petromyzon. Jour. Morph., 1.

SEDGWICK, A. 1892 Notes on elasmobranch development. Quart. Jour. Micr. Sci., vol. 33.

1894 On the inadequacy of the cellular theory of development, and on the early development of nerves, particularly of the third nerve and of the sympathetic in Elasmobranchii. Quart. Jour. Micr. Sci., vol. 37.

SEWERTZOFF, A. N. 1895 Die Entwickelung der Occipitalregion der niederen Vertebraten im Zusammenhang mit der Frage über die Metamerie des Kopfes. Bull. Soc. Imp. Nat. Muscou., Heft. 2.

1898 a Die Metamerie des Kopfes von Torpedo. Anat. Anz., Bd. 14.

1898 b Studien zur Entwicklungsgeschichte des Wirbeltierkopfes. 1. Die Metamerie des Kopfes des elektrischen Rochen (Fortsetzung). Bull. Soc. Imp. Nat. Moscou, N. S., T. 12.

SHIPLEY, A. E. 1887 On some points in the development of Petromyzon fluviatilis. Quart. Jour. Micr. Sci., vol. 27.

SHORE, T. W. 1889 On the minute anatomy of the vagus nerve in selachians with remarks on the segmental value of the cranial nerves. Jour. Anat. and Physiol., vol. 23.

SHOREY, M. LOUISE 1909 The effect of the destruction of peripheral areas on the differentiation of the neuroblasts. Jour. Exp. Zool., vol. 7.

STANNIUS, H. 1849 Das peripherische Nervensystem der Fische, anatomisch und physiologisch untersucht. Rostock.

Digitized by Google

STEINACH, E. 1893 Ueber die motorische Innervation des Darmtractus durch die hinteren Spinalnervenwürzeln. Lotos, N. F., Bd. 14.
1895 Motorische Functionen hinterer Spinalnervenwürzeln (in collaboration with H. Wiener). Arch. ges. Phys., Bd. 60.

STREETER, G. L. 1905 The development of the cranial and spinal nerves in the occipital region of the human embryo. Amer. Jour. Anat., vol. 4.
1908 The nuclei of origin of the cranial nerves in the 10 mm. human embryo. Anat. Rec., vol. 2.

STRONG, O. S. 1890 The structure and homologies of the cranial nerves of the amphibia, as determined by their peripheral distribution and internal origin. Zool. Anz., Bd. 13.
1895 The cranial nerves of amphibia. Jour. Morph., vol. 10.
1903 The cranial nerves of Squalus acanthias. Science, vol. 17.

VON SZILY, A. 1904 Zur Glasskörperfrage. Anat. Anz., Bd. 24.

TRETJAKOFF, D. 1909 Das Nervensystem von Ammocoetes. 2. Das Gehirn. Arch. f. micr. Anat., Bd. 74.

VAN VALKENBURG, C. T. 1910 Nucleus facialis dorsalis, nucleus trigemini posterior, nucleus trochlearis posterior. Könink. Akad. Wetensch. te Amsterdam.

VAN WIJHE, J. W. 1883 Ueber die Mesodermsegmente und die Entwickelung der Nerven der Selachierkopfes. Naturk. Verh. d. K. Akad. Wiss. Amsterdam, Bd. 22.
1886 a Ueber Somiten und Nerven im Kopfe von Vögel- und Reptilienembryonen. Zool. Anz., Bd. 9.
1886 b Ueber die Kopfsegmente und die Phylogenie des Geruchsorgans der Wirbelthiere. Zool. Anz., Bd. 9.
1889 a Ueber die Mesodermsegmente des Rumpfes und die Entwickelung des Excretionssystems bei Selachiern. Arch. mikr. Anat., Bd. 33.
1889 b Die Kopfregion der Kranioten beim Amphioxus, nebst Bemerkungen über die Wirbeltheorie des Schadels. Anat. Anz., Bd. 4.

VIGNAL, W. 1883 Mémoire sur le développement des tubes nerveux chez les embryons des mammifères. Arch. de physiol. norm. et path., tom. 1.
1888 Recherches sur le développement des elements des couches corticales du cerveau et du cervelet chez l'homme et les mammifères. Arch. physiol. norm. et path., tom. 2.

WALDEYER, W. 1891 Ueber einige neuere Forschungen im Gebiete der Anatomie des Zentralnervensystems. Deutsche med. Wochenschr., Bd. 17.

WATERS, B. H. 1891 Some additional points on the primitive segmentation of the vertebrate brain. Zool. Anz., Bd. 14.
1892 Primitive segmentation of the vertebrate brain. Quart. Jour. Micr. Sci., vol. 33.

WEBER, A. 1900 Contribution à l'étude de la metamérie du cerveau anterieur chez quelques oiseaux. Arch. d'Anatomie Microscop.

WIEDERSHEIM, R. 1880 Das Gehirn von Ammocoetes und Petromyzon planeri u. s. w. Morph. Stud., Bd. 1.

WILLEY, A. 1894 Amphioxus and the ancestry of vertebrates. New York.

Digitized by Google

WILSON, J. T., AND HILL, J. P. 1907 On the development of Ornithorhynchus. Phil. Trans. Roy. Soc., London, vol. 199.

WLASSEK, R. 1898 Die Herkunft des Myelins. Ein Beitrag zur Physiologie des nervösen Stützgewebes. Arch. f. Entwick.-Mechan., Bd. 6.

WORKMAN, J. S. 1900 The ophthalmic and eye-muscle nerves of the catfish (Ameiurus). Jour. Comp. Neur., vol. 10.

ZIEGLER, H. E. 1908 a Die phylogenetische Entstehung des Kopfes der Wirbelthiere. Jena. Zeitschr. f. Naturw., Bd. 43.

1908 b Ein Embryo von Chlamydoselachus anguineus Garm. Anat. Anz., Bd. 33.

ZIEHEN, TH. 1906 Die Histogenese von Hirn- und Rückenmark. Entwickelung der Leitenbahnen und der Nervenkerne bei den Wirbelthiere. Handbuch d. vergl. u. exp. Entwickelungslehre der Wirbeltiere, Bd. 2.

ZIMMERMANN, W. 1891 Ueber die Metamerie des Wirbelthierkopfes. Verh. Anat. Gesellsch. München.

1899 Ueber Kopfhöhlerudimente beim Menschen. Arch. f. mikr. Anat., Bd. 53.

ABBREVIATIONS

I *to* VIII, neuromeres or encephalomeres
1 to 9, somites of VanWijhe
1^d to 6^d, dorsal divisions of myotomes 1 to 6
1^v to 6^v, ventral divisions of myotomes 1 to 6
V.md., ramus mandibularis trigemini
V.mx., ramus maxillaris trigemini
V.opt.su., ramus ophthalmicus superficialis trigemini
V.opt.p'fnd., ramus ophthalmicus profundus trigemini
VIrec., ramus recurrens abducens
VIIac., ramus acusticus facialis
VIIbuc., ramus buccalis facialis
VIIhoi., ramus hyoideus facialis
VIIopt.su., ramus ophthalmicus superficialis facialis
a., 'anterior' somite of Miss Platt
abd., abducens nerve anlage
ao.d., dorsal aorta
arc.vsc., visceral arch
ax., axone process
cd.d., chorda dorsalis
ch.dors., dorsal chiasma
cl.crs.n., neural crest cells
cl.n'bl., neuroblast cell.
cl.R.B., Rohon-Beard cell
d.pro., pronephric duct
ec'drm., ectoderm
en'drm., entoderm
fis.vsc., visceral clefts
gls.phy., glossopharyngeus
gn.dors., dorsal ganglion
gn.opt.pf'nd., ganglion of the r. ophthalmicus profundus
gn.sym., sympathetic ganglion
gn.vag., vagus ganglion
hyp.,[1] first, or transient, root of hypoglossus
l., lens
la.ct., cutis plate
la.mu., muscle plate
m., mouth
ms'ec'drm., mesectoderm
ms'ench., mesenchyma
ms'en'drm., mesentoderm
mb.cl., cell membrane
mb.lim., limiting membrane
mu.hyp., hypoglossus musculature
mu.obl.sup., superior oblique muscle

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my., myotome
my.$^{1,2,3-8}$, myotomes of VanWijhe's somites 1 to 8
my.^{2dl}., dorso-lateral division of the second myotome
my.^{2vl}., ventro-lateral division of the second myotome.
my.^{2m}., median division of the second myotome
my.^{4dl}., dorso-lateral division of the first post-otic myotome
my.^{4vl}., ventro-lateral division of the first post-otic myotome
my.^{4m}., median division of the first post-otic myotome
n., olfactory pit
nidl., nidulus, or 'motor nucleus' of nerve
nidl.abd., nidulus of abducens nerve
nidl.oc., nidulus of oculomotor nerve
nidl.tr'ch., nidulus of trochlearis nerve
n'v.^{1}, first post-otic nerve in Petromyzon
n'v.^{2}, second post-otic nerve in Petromyzon
oc'mot., oculomotorius nerve anlage
ot., otic vesicle
pl., plasma
rx.d., fiber bundle of dorsal nerve
rx.v., fiber bundle of ventral nerve
scl., sclerotome
so., somite
sp., spiracle
subch., sub-chordal rod
tb.n., neural tube
thyr., thyreoid
tr'ch., trochlearis
tr'ch.dors., dorsal branch of the trochlearis nerve
tr'ch vent., ventral branch of the trochlearis nerve
tr.art., truncus arteriosus
vac., vacuole
vag., vagus nerve
vn.crd., cardinal vein
vs.opt., optic vesicle

PLATE 1

EXPLANATION OF FIGURES

All the figures of this plate were drawn with Abbe camera, one-twelfth homogeneous oil immersion objective and No. 6 compensation ocular of Zeiss. In reproduction the magnification has been reduced by one-third. The series of drawings illustrates the stages just preceding and following the appearance of the anlagen of somatic motor nerves in the trunk region of Squalus embryos.

1 A portion of a cross-section (DK 2-3-10) of a Squalus embryo with eight somites (Stage D of Balfour) in the middle trunk region showing the relations of neural tube, somite, and chorda. The absence of plasmodesmata or protoplasmic strands connecting neural tube and somite is to be noted. A vacuolated plasma fills the intercellular space between the neural tube and the myotome.

2 A portion of a cross-section (IK 3-2-37) of a Squalus embryo of 6 mm. (Balfour's Stage I) in the middle of the trunk region, showing the conditions just previous to the appearance of a ventral nerve anlage. The section is taken from an embryo of about twice the length of the one from which figure 1 was drawn. The section shows no indication of protoplasmic or nervous connection between the neural tube and the somite. The outflow of processes from the sclerotome cells (*scl.*) is the beginning of the movement of mesenchymatous cells

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into the region between myotone and neural tube. The anlagen of the somatic motor nerves of the myotomes immediately anterior to the one shown in the section have already made their appearance as protoplasmic outflows from the neural tube, an outflow which is correlated with a movement of the sclerotome cells.

3 A portion of a cross-section (II 5–3–12) of a Squalus embryo of 7 mm. (Balfour's Stage I) in the cloacal region, showing the relations of neural tube and somite immediately before the appearance of a somatic motor nerve. Nervous, or protoplasmic, connection of neural tube and myotome has already been effected in the metameres just anterior to the one from which this section was taken. The deeper staining properties of the cell (*cl.n'bl.*) may indicate that it is a neuroblast about to extend a process toward the somite. The migration of the mesenchyma cells from the sclerotome has already begun. This and figures 1 and 2 show that before outflows of neuroblastic cells make their appearance there is no protoplasmic connection between the nervous and muscular systems. In the intercellular space between the two, however, may be demonstrated a dilute, plasmoid substance containing a minimal amount of vacuolated coagulable substance more resistant to stains than the cellular protoplasm. To show it at all in a drawing greatly exaggerates its visibility.

4 A cross-section (IL 4–3–11) of a Squalus embryo of 7 mm. (Stage I of Balfour) in the trunk region just anterior to the cloaca, showing a very early stage of protoplasmic connection between neural tube and myotome, established by an amoeboid outflow of a single neuroblast cell of slightly deeper staining properties than those of the surrounding cells. The pseudopodial processes extend in various directions toward the somite and show finer branches which have connections with the vacuoles of the intercellular plasmoid substance. That the processes are genetically related to the neuroblastic cell, however, is evinced by their staining properties.

5 A portion of a cross-section (IL 4–2–1) of the same embryo as the one shown in figure 4 in the second metamere anterior to it. At least two cells appear to participate in the protoplasmic outflow from the neural tube. Focussing brings out the fact that the amoeboid processes extend antero-posteriorly along the surface of the myotome as well as dorso-ventrally. The neuroblast shows the characteristic deeper staining qualities of the neuroblast cell.

6 A portion of a cross-section of the same embryo as figures 4 and 5. The section (IL 4–2–14) is through the metamere immediately posterior to that in figure 5 and anterior to that in figure 4. As compared with figure 5, the amoeboid processes seem further extended and the limiting membrane of the neural tube seems interrupted for a greater extent than in the sections anterior and posterior. The outer boundaries of at least three cells are extended beyond the limiting membrane of the neural tube.

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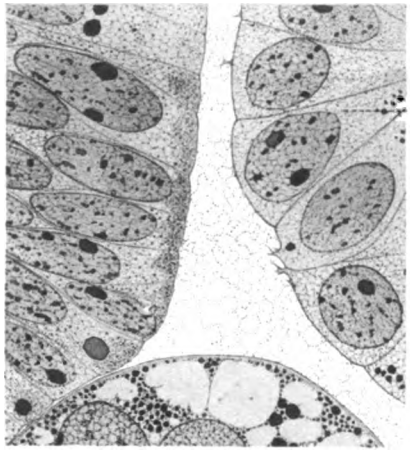

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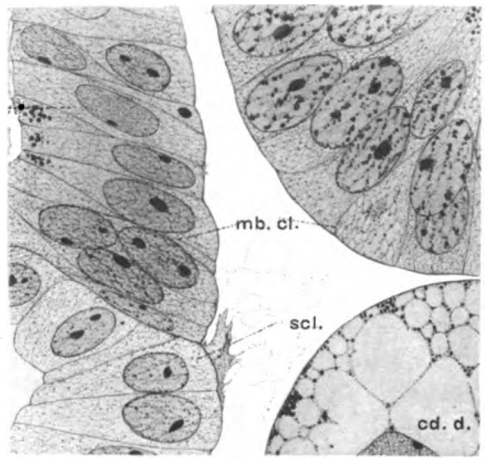

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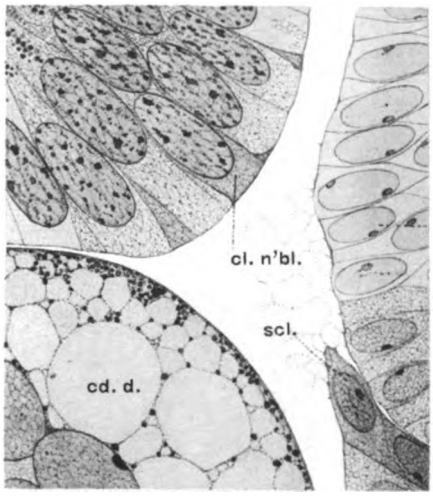

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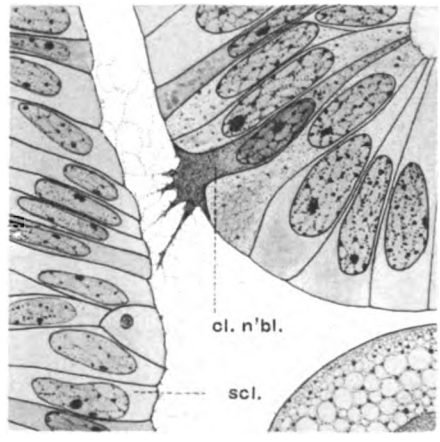

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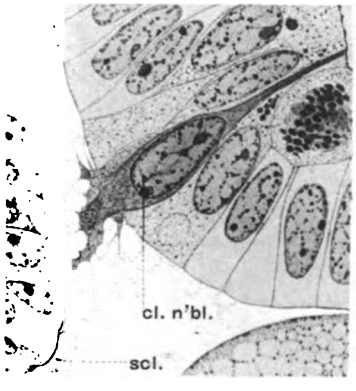

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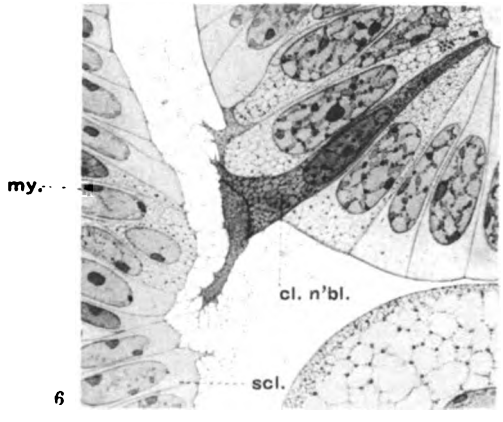

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PLATE 2

EXPLANATION OF FIGURES

All the figures of this plate were drawn with the same lenses, etc., as those of plate 1. In reproduction the magnification has been reduced one-third. The series illustrates stages in the development of the anlagen of spinal somatic motor nerves in Squalus embryos up to the time of migration of medullary cells into the nerve.

7 A portion of a cross-section (IL 4–2–17) of a Squalus embryo of 7 mm. (Stage I of Balfour) of the same series as those shown in figures 4, 5 and 6, showing the anlage of the somatic motor nerve of the same metamere as that in figure 6 but of the opposite side of the body and three sections posterior. The evidence that the protoplasmic connection between the neural tube and somite is a derivative of the neural tube is the same as that shown in the earlier figures. The section also shows a protoplasmic outflow from a cell in the lateral wall of the neural tube. Such outflows are exceptional and do not appear to persist in later stages.

8 and 9 Portions of two adjacent sections (II 5–2–17 and II 5–2–18) in the cloacal region of a 7 mm. embryo, showing an early stage in the development of a plasmodesm or anlage of a somatic motor nerve. The protoplasmic connection between the neural tube and the myotome consists of two elements, one derived from the neural tube, that is, a portion composed of the processes of neuroblasts (*cl.n'bl.*) labeled *ax.* in the figure, and the other consisting of migrant cells from the sclerotome of the somite (*scl.*). The two elements are readily distinguishable in the sections, since the processes of the neuroblastic cells stain more deeply than the sclerotome cells and the limiting membranes of the cells are shown distinctly.

10 A portion of a cross-section (IL 4–1–30) of a 7 mm. embryo in the middle trunk region where the myotome and sclerotome lie somewhat nearer the neural tube than in the caudal region. The protoplasmic bridge between neural tube and myotome consists of the processes of medullary neuroblasts which extend between the myotome and sclerotome along the median surface of the myotome. A comparison with earlier stages shows that the bridge is not a primary one, as thought by Held ('06) and Paton ('07), but secondary.

11 A portion of a cross-section (II 5–1–13) of a 7 mm. embryo, showing a somatic motor nerve anlage in a stage of development somewhat more advanced than that shown in figure 10. Processes of medullary neuroblasts may be traced for some distance along the median surface of the myotome, between the sclerotome and the myotome. The more deeply staining properties of the distal portions of the axone processes are noteworthy, in connection with the problem of the origin of the neurofibrillae. The stage corresponds essentially with Paton's ('07) figure 2. The difference in the phenomena and resultant difference in interpretation may be ascribed largely to the difference in the methods of staining and of preservation. What Paton regards as a neurofibril arising in the myotome independently of the nervous system is actually, as shown in sections of embryos preserved by the vom Rath method, the distal portion of the neuraxon process of a medullary neuroblast. Instead of appearing within the myotome as stated by Paton, the actual position, as seen in figure 11, is between the myotome and sclerotome. The results obtained by Paton's excellent method of staining the neurofibrillae need to be controlled by a comparison with methods which, like that of vom Rath, bring out the cell boundaries.

12 A portion of a cross-section (IL 3–2–42) of a 7 mm. embryo, showing an early stage in the process of migration of medullary cells into a somatic motor nerve anlage in the middle trunk region. Evidence has been given in a former paper ('03) that these cells are chiefly, if not entirely, concerned in the process of formation of the neurilemma of the somatic motor fibers. As shown in the figure, the breaking up of the sclerotome into loose mesenchyma has already begun. The relation of the fibrillar portion of the nerve anlage to neuroblasts in the neural tube is not shown in the section, a result of the bending of the axones upon their emergence from the neural tube.

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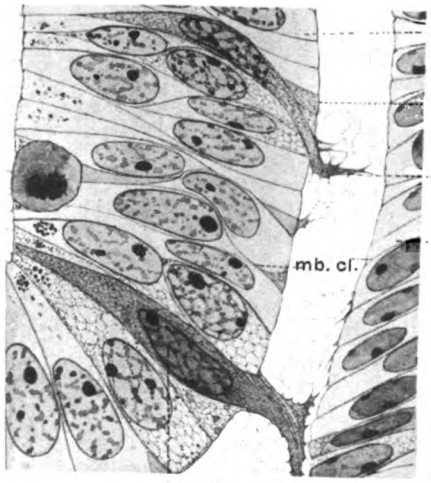

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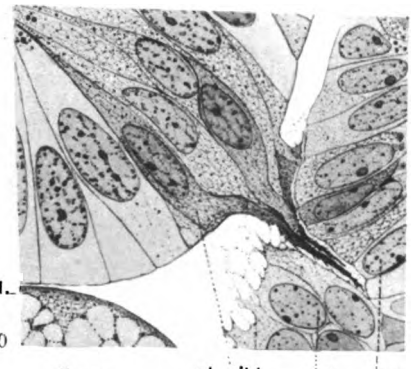

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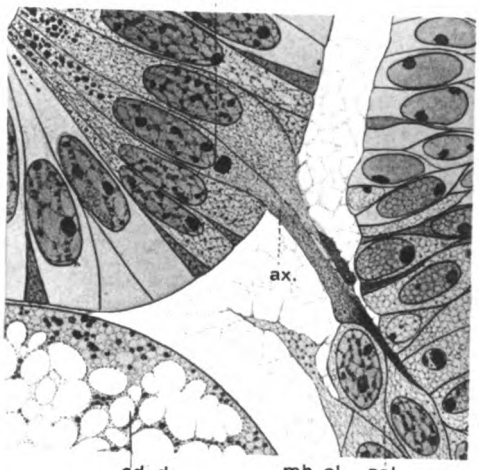

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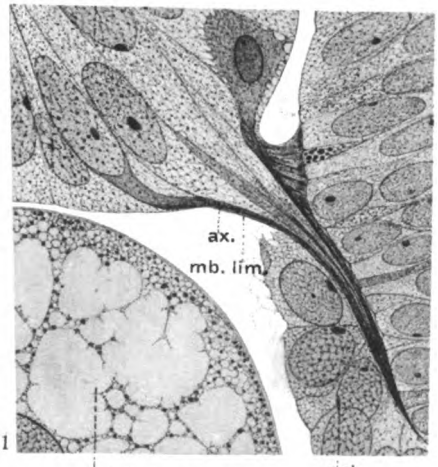

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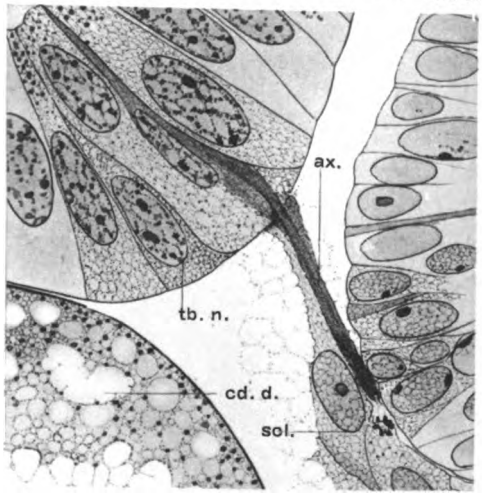

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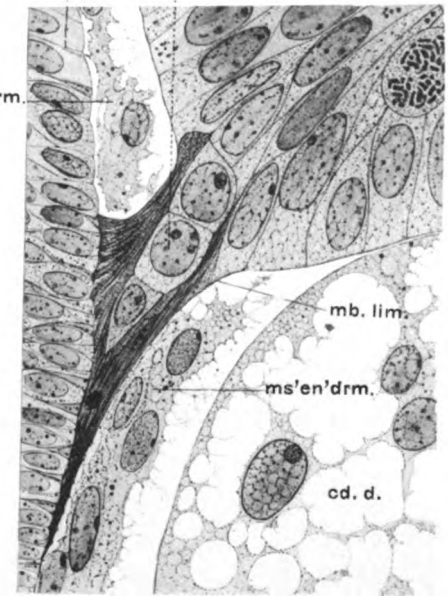

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PLATE 3

EXPLANATION OF FIGURES

All the figures of this plate were drawn in the same way as those on plates 1 and 2. Magnification reduced one-third in reproduction. The series of figures on this and the following plate illustrate stages in the extension of the neuraxon processes of the Rohon-Beard cells. The phenomena appear analogous with those shown in the formation of the anlagen of ventral motor nerves (plates I and II).

13 A portion of a cross-section (IJ 4–1–22) of a 6 mm. embryo in the middle trunk region. A portion of the ectoderm and of the dorsal wall of the neural tube are shown. The amoeboid process (*pl.*) of a medullary cell is strikingly similar to those which form the ventral nerve anlagen. Finer branches of the protoplasmic processes show definite relations to the vacuolated intercellular plasma, but no evidence that this relation is a genetic one. The phenomena are entirely in harmony with the supposition that the amoeboid protoplasmic process has a genetic relation to the medullary cell. Earlier stages show no evidence of protoplasmic continuity between neural tube and ectoderm.

14 A portion of a cross-section (IK 2–6–37) of a 6 mm. embryo in the middle trunk region, showing a portion of the dorso-lateral wall of the neural tube and a Rohon-Beard cell with deeply stained neuraxon process extending beyond the limiting membrane of the neural tube. Similar outflows of adjacent cells may also be seen, and the phenomena strikingly resemble those presented in the formation of the somatic motor nerves (plates 1 and 2).

15 A portion of a cross-section (sections IK 2–3–22 and IK 2–3–23 combined) of a 6 mm. embryo in the middle trunk region, showing a part of the dorso-lateral wall of the neural tube and the greatly elongated neuraxon process of a Rohon-Beard cell which may be traced through the wall of the neural tube into the plasma-filled space between the neural tube and the ectoderm. The pseudopodia-like extensions of the distal extremity of the neuraxon show relations to the vacuolated plasma, but such evidence does not prove any genetic relationship between the two, nor a primary protoplasmic relationship between the neuroblast cell and its peripheral distribution.

16 A portion of a cross-section (sections II 5–1–31, II 5–1–32 and II 5–1–33 combined) of a 6 mm. embryo in the middle trunk region, showing the dorso-lateral wall of the neural tube and the neuraxon processes of two adjacent Rohon-Beard cells, one of which extends into the space between myotome and ectoderm the other between myotome and neural tube, the neuroblast cell of the latter not shown. The neuraxon processes appear distinctly fibrillar only in the proximal portion. Since the distribution of these neuraxon processes in later stages is essentially the same, viz., the extra-embryonic ectoderm, the different relations to the dorsal part of the myotome appears to favor the view that the path by which a neuraxon finds its way to its terminal organ is a matter of chance rather than a predetermined one along an intercellular bridge. Moreover, the amoeboid processes do not extend in one direction, as would seem demanded by the latter assumption, but irregularly in different directions.

17 to 20 (See p. 170).

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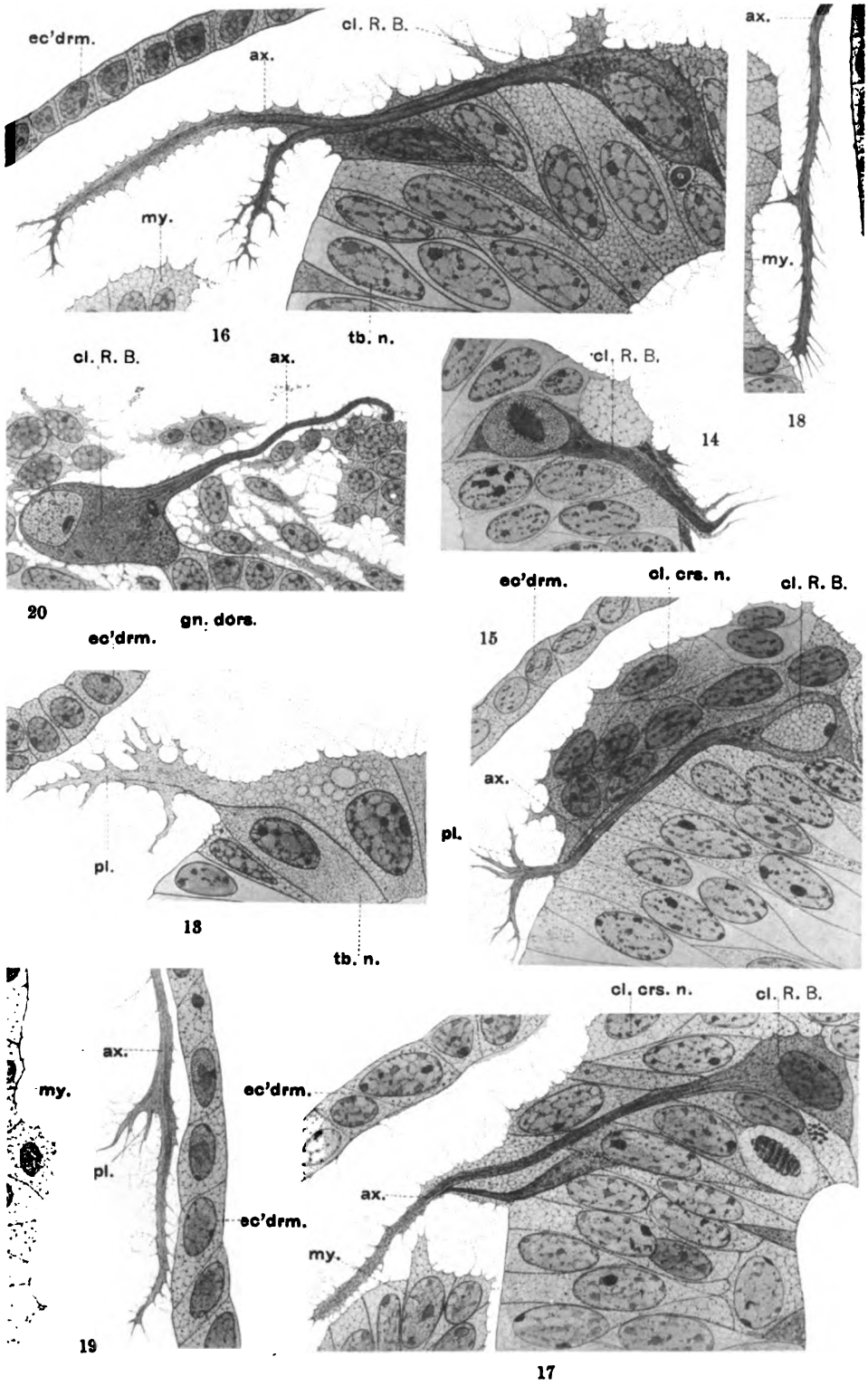

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17 A portion of a cross-section (sections IK 2-4-15 and IK 2-4-16 combined) of a 6 mm. embryo in the middle trunk region, showing the processes of two Rohon-Beard cells, one of which lies out of the plane of the section. The conditions resemble those shown in figure 16, except that the processes appear confluent instead of divergent. The neurofibrillae are well differentiated in the proximal portion of the neuraxon.

18 and 19 Portions of cross-sections (IK 2-5-6 and IK 2-5-37) of a 6 mm. embryo in the middle trunk region, showing the distal termination of the growing neuraxon process of a Rohon-Beard cell as it extends into the space between the myotome and the ectoderm. In the case of the process in figure 18 the growing end lies nearer the myotome, while in figure 19 the growing end lies nearer the ectoderm. Comparison with earlier stages shows that in this region there are no protoplasmic bridges in the region shown in the drawing—the intercellular spaces are filled with an unstained vacuolated plasma. The brush-like termination is a characteristic feature of the neuraxon process.

20 A portion of a cross-section of a 7 mm. embryo in the middle trunk region, showing a Rohon-Beard cell on the top of a spinal ganglion. Its deeply staining neuraxon process contrasts strongly with the surrounding mesenchyma, and the evidence of the genetic relation of ganglion cell and neuraxon process seems more convincing than in the case of the cells which are imbedded in the wall of the neural tube. The process may be traced to a point lateral to the myotome. The section figured however does not show the peripheral termination of the process, which bends out of the plane of the section.

PLATE 4

EXPLANATION OF FIGURES

21 and 22 Portions of cross-sections of 6 mm. embryos in the middle trunk region, showing Rohon-Beard cells in somewhat advanced stages of the extension of the neuraxon processes. Figure 21 is a combination drawing from three sections (II 4-4-26, 27, 28). Figure 22 is a combination of two sections (IK 2-6-29, 30). The presence of neurofibrillae in the protoplasmic processes evinces their nervous character. The distal extremity of these neuroblast processes, however, is granular, vacuolated and extended into pseudopodial processes. Figure 21 does not appear to harmonise with the assumption of predetermined paths for the extension of the nervous outgrowths, but rather with the view that neuraxons are pseudopodia-like outgrowths of neuroblasts. The variation in the form of the amoeboid termination of the neuraxon processes shown in the two figures is striking and significant.

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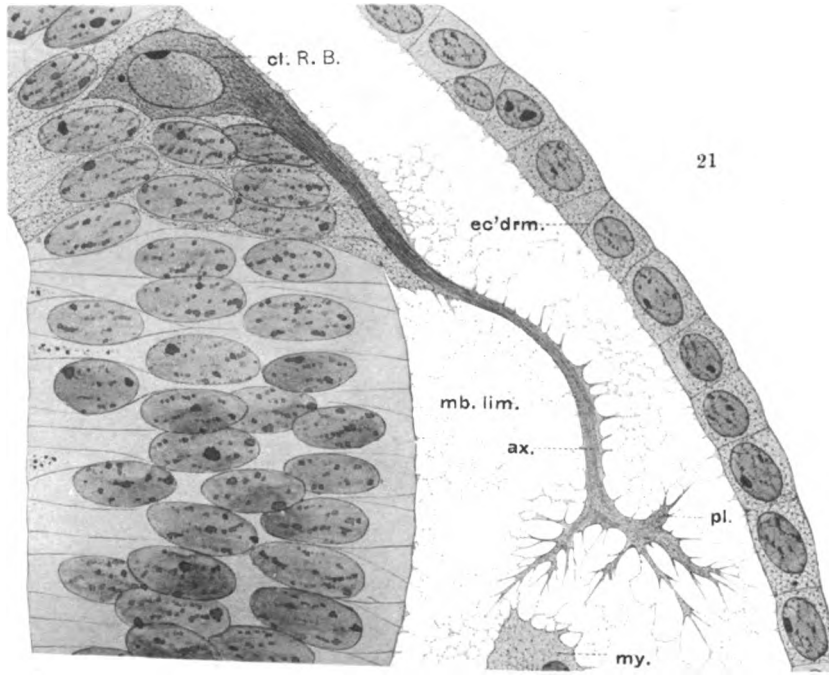

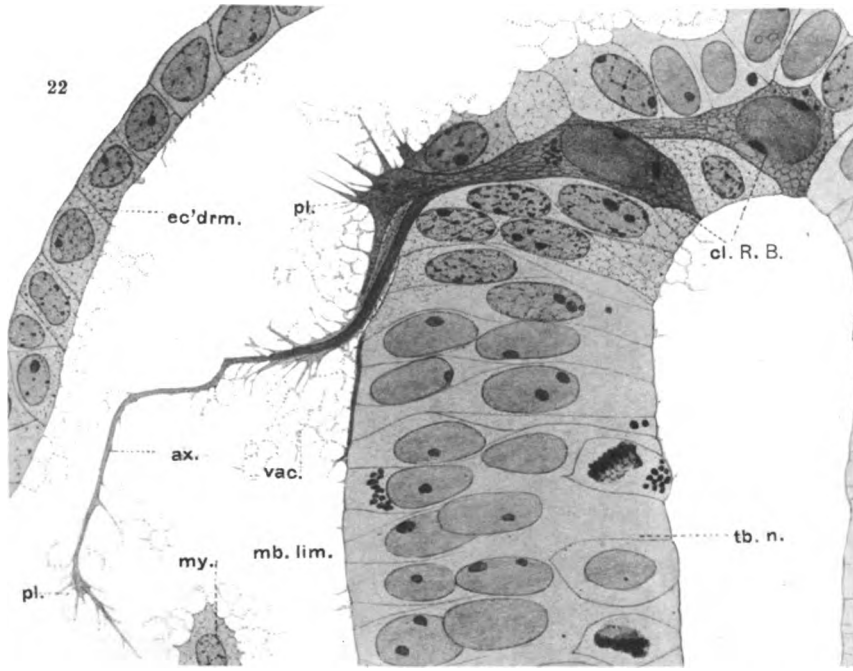

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PLATE 5

EXPLANATION OF FIGURES

All the figures are based on camera drawings. Figures 23 to 28 inclusive are a series of semi-diagrammatic drawings, illustrating the more important stages in the development of spinal somatic motor nerves and summarizing the essential features of the histogenesis of spinal ventral nerves. Figures 29 and 30 are camera drawings of spinal nerves with one-twelfth homogeneous oil-immersion objective, No. 6 compensation ocular of Zeiss, and camera lucida of Abbe. Reduction one-third in reproduction.

23 A semi-diagrammatic drawing of a portion of a cross-section (IH 1–6–9) of a 6 mm. embryo in the region of the cloaca. The anlage of the somatic motor nerve is seen as a structure consisting of the protoplasmic processes of neuroblasts in the ventrolateral wall of the neural tube. The migration of the mesenchyma of the sclerotome has already begun.

24 A portion of a cross-section (IE 2–1–last), of a 9 mm. embryo in the caudal region, showing a somewhat more advanced stage in the development of a ventral nerve. The neuraxon processes of the medullary neuroblasts have extended farther along the median surface of the myotome and the mesenchyma cells have advanced to a point nearer the neural tube.

25 A semi-diagrammatic drawing of a cross-section (IE 2–7–27) of a 7 mm. embryo in the middle trunk region, showing the beginning of the migration of medullary cells into the anlagen of somatic motor nerve and neural crest. The relation of the fibrillar portion of the somatic motor nerve to neuroblasts is shown in the figure.

26 A semi-diagrammatic drawing of a portion of a cross-section (IH 2–1–20) of a 9 mm. embryo in the trunk region showing a somewhat more advanced stage in the development of a somatic motor nerve. Medullary cells are still in the process of migration from the neural tube along the nerve anlage. The ganglion of the dorsal nerve has been formed by the migration and aggregation of neural crest cells between myotome and neural tube. A Rohon-Beard cell in an early stage of formation of a neuraxon process appears in the dorsal wall of the neural tube.

27 A semi-diagrammatic drawing of a cross-section (KJ 3–4–middle) of an 11 mm. embryo in the middle trunk region, showing a more advanced stage in the differentiation of a somatic motor nerve. The emigrated medullary cells at this stage form a sheath enclosing the fibrillar portion of the nerve. Neuroblasts have become differentiated within the dorsal ganglion. A Rohon-Beard cell with neuraxon process extending between myotome and ectoderm is shown.

28 A semi-diagrammatic drawing of a cross-section (LAB 5–3–17) in the middle trunk region of a 17 mm. embryo, showing a stage in the development of a somatic motor nerve, when the anlage of a sympathetic ganglion has made its appearance at a point opposite the dorsal aorta and median to the trunk of the spinal nerve of the metamere. At this stage fibrous connection of the dorsal ganglion with the neural tube has been established and both dorsal and ventral rami have reached a considerable extent in their development. The migration of medullary cells into the somatic motor root has ceased. The cells that have

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wandered into the nerve anlage form a sheath around the fibrillar part of the nerve. The section shows a Rohon-Beard cell with neuraxon entering the root of the dorsal nerve—a rather exceptional relation.

29 A cross-section of a spinal nerve (MM 21-2-4) of a 46 mm. Squalus embryo, showing the fibrillar portion of the nerve consisting of deeply stained fibrils and a surrounding layer of sheath cells, presumably of medullary origin. The neuraxon fibers of the sensory bundle are somewhat larger in diameter than those of the motor bundle. Both appear as highly refractive granules, separated by a somewhat vacuolated intercellular plasma.

30 A cross-section of a spinal nerve in a 17 mm. embryo, showing sensory and motor components at the level of a sympathetic ganglion. The motor bundle lies nearer the myotome than does the sensory bundle, and each is surrounded by a single layer of sheath cells. The sympathetic ganglion anlage lies median to and somewhat between the two.

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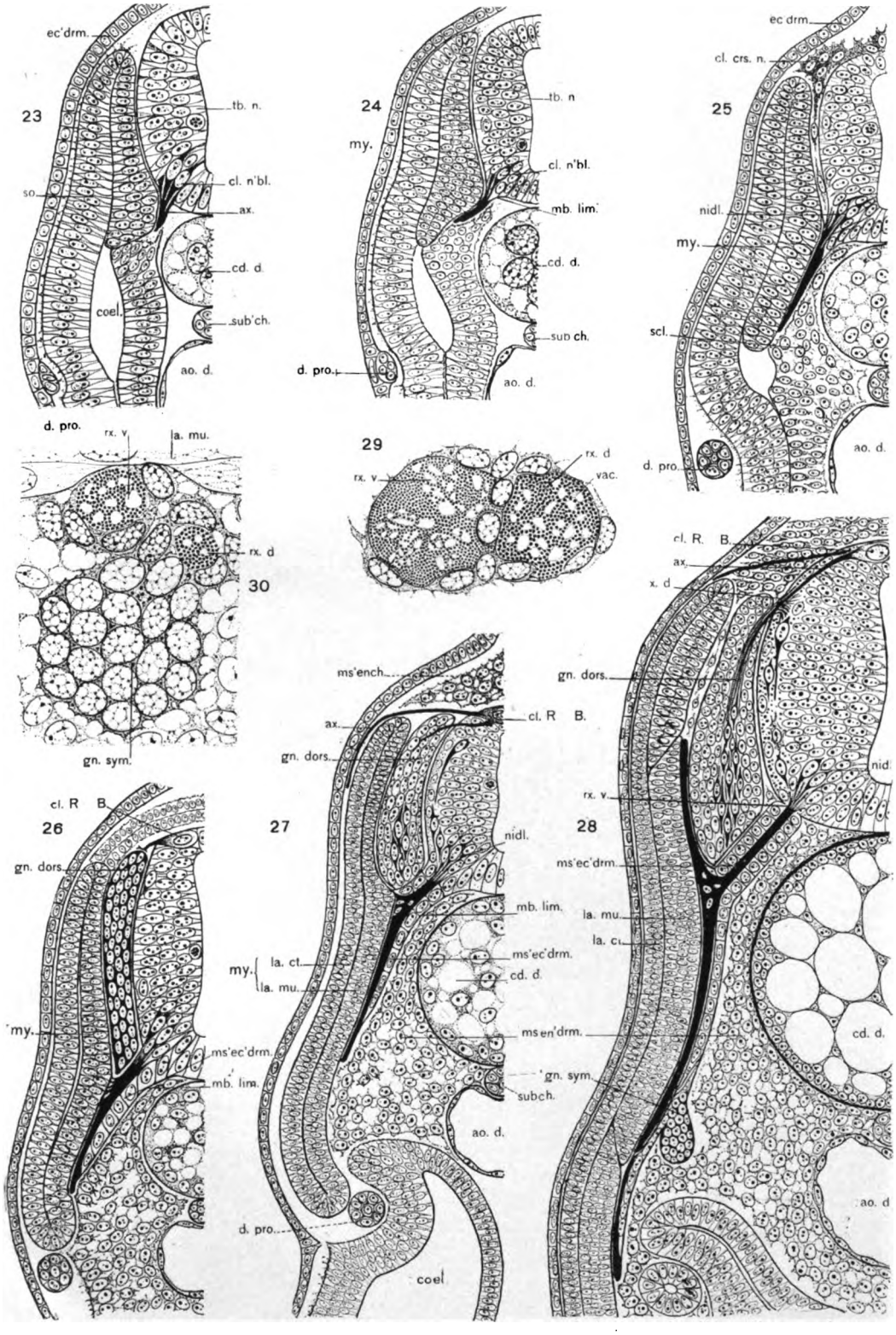

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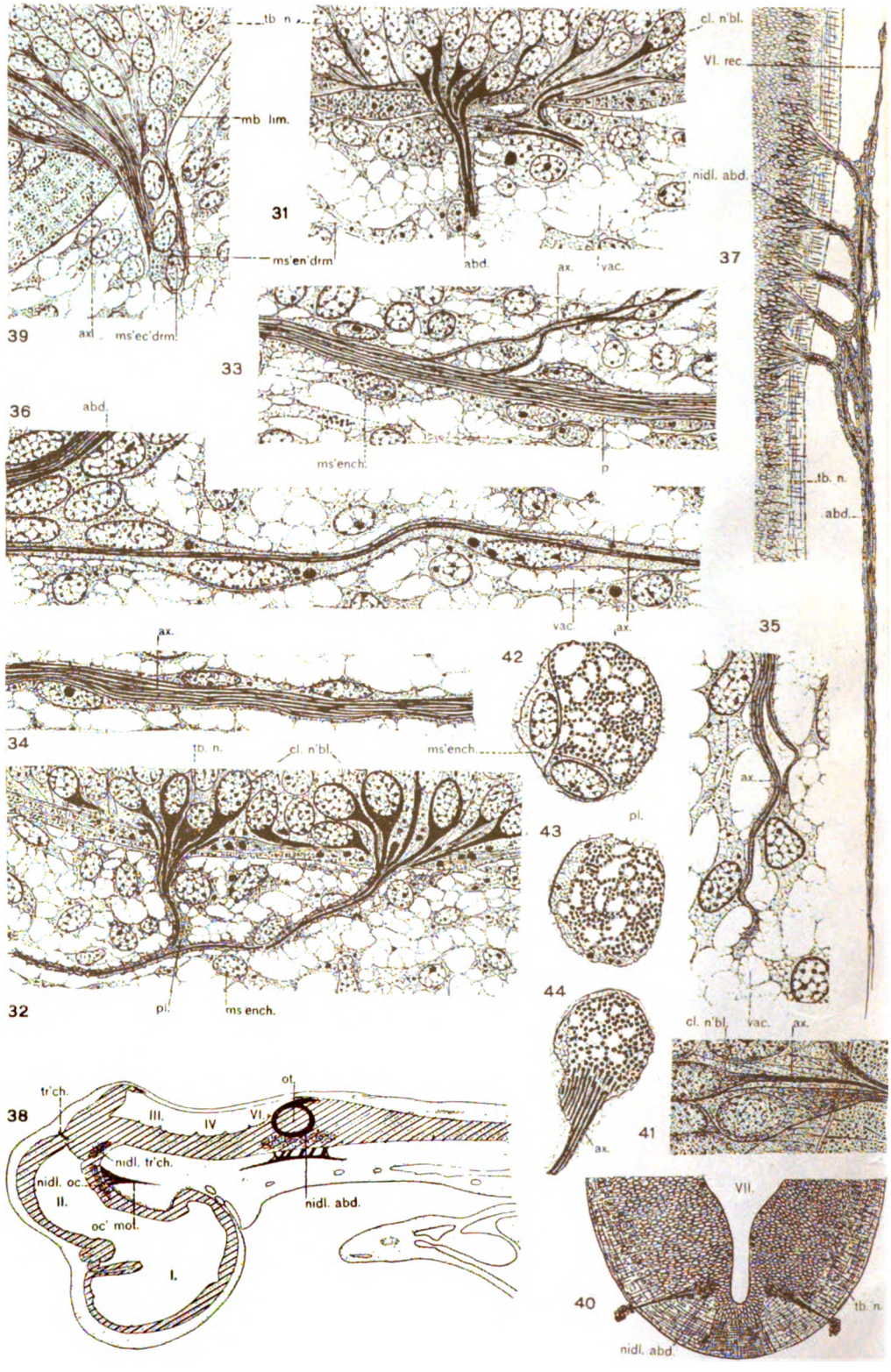

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PLATE 6

EXPLANATION OF FIGURES

A series of camera drawings illustrating the histogenesis of the abducens nerve With the exception of figures 37, 38 and 40, all were drawn with one-twelfth homogeneous oil-immersion objective and compensation ocular 6 or 8 of Zeiss.

31 A portion of a parasagittal section (KP 2–1–6) of a 10 mm. embryo, showing an early stage in the development of the abducens anlage, which makes its appearance as a product of the union of the processes of neuroblasts in the ventrolateral wall of the medulla immediately posterior to the otic capsule. The presence of loose mesenchyma in the region of the nerve anlage complicates the picture, but the processes of deeply stained neuroblasts may easily be traced into the nerve anlage. The mesenchyma cells are granular, much vacuolated, and stain lightly, showing in some cases protoplasmic connections with the abducens anlage. In every essential respect the picture resembles an early stage in the histogenesis of a spinal somatic motor nerve. The chief differences consist in the relatively early appearance of a loose mesenchyma and in the remoteness of the myotome from the point of emergence of the neuraxon processes of the nerve anlage. The presence of a lightly staining granular protoplasm surrounding the deeply stained processes of the neuroblasts is noteworthy, but it is difficult to determine whether this ensheathing protoplasm is of mesenchymatous or medullary in origin. Analogy with spinal nerves would favor the conclusion that it is an outflow from medullary cells.

32 A portion of a parasagittal section (KR 1–3–4, 5, 6)—strictly, a combination of three sections—of an 11 mm. embryo, showing the anlage of the abducens nerve, when it possesses two roots and when its growing tip extends for some distance anteriorly in the mesenchyma lying at the base of the medulla. Deeply stained processes of medullary neuroblasts may be traced into the nerve anlage with its sheath of granular protoplasm. The highest powers of the microscope fail to resolve the neuraxon processes into constituent neurofibrils. As no evidence of the migration of medullary elements into the nerve anlage appears in this or in preceding stages, the cells in the vicinity of the nerve anlage are presumably mesenchymatous.

33 A portion of a parasagittal section (KS 2–2–7) of an 13 mm. embryo, showing a portion of the abducens anlage in a later stage of development than in figure 32. The nerve anlage consists at this stage of a compact bundle of deeply stained neuraxons surrounded more or less completely by a sheath of mesenchymatous cells. The section is somewhat exceptional in showing two isolated neuraxons which join the nerve anlage and each of which consists of a deeply stained fibril surrounded by a very thin, lightly stained granular protoplasmic sheath. Each of the neuraxons is also associated with a nucleus presumably of mesenchymatous origin.

34 A portion of a parasagittal section (LAA 2–1–3) of a 19 mm. embryo, showing a peripheral portion of the abducens anlage, consisting of a bundle of highly refractive neuraxons surrounded by a sheath of mesenchymatous cells and granular protoplasm.

35 to 44 (See pp. 178 and 179).

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35 A portion of a parasagittal section (LB 2-2-6) of a 17 mm. embryo, showing the peripheral termination and growing tip of the abducens nerve anlage at a stage when it has nearly reached the posterior rectus muscle. The amoeboid termination closely resembles those of somatic motor spinal nerves and of the Rohon-Beard cells, and the section thus strongly favors the outgrowth theory of nerve histogenesis and the opinion that the abducens in its histogenesis resembles the spinal somatic motor nerves.

36 A portion of a parasagittal section (LK 2-2-10) of a 19.25 mm. embryo showing a portion of the abducens anlage in the vicinity of its point of emergence from the medulla. The section is of interest chiefly because it shows a single deeply stained fibril surrounded by a sheath of spindle-shaped cells. It was such evidence as this that led Dohrn ('91) at one time to infer that the spindle-shaped cells were genetically related to the neuraxon fiber. The evidence presented in this paper, however, tends to show that there is no genetic relation between the fiber and its surrounding cellular sheath. At this stage of development of the nerve anlage the process of migration of medullary cells has already begun and the ensheathing cells shown in the figure may be of medullary origin.

37 A graphic reconstruction of the anlage of the abducens nerve as seen in parasagittal sections of a 19 mm. embryo. The nerve arises from the base of the seventh and eighth brain neuromere (Neal), four roots emerging from the seventh and one only from the eighth. Its connection with these two distinct segments of the brain suggests the inference that the abducens is the nerve of at least two metameres. The posteriorly directed ramus recurrens of the abducens also suggests that the nerve was once distributed to musculature posterior to that which it now innervates. This branch soon atrophies. The roots of the nerve show a tendency to form a network or plexus.

38 A semi-diagrammatic drawing based on a parasagittal section through the head of a 19 mm. embryo, intended to show the position of the niduli of the eye muscle nerves. The niduli of the oculomotorius and of the trochlearis belong to adjacent metameres, while the nidulus of the abducens is several neuromeres removed.

39 A portion of a cross-section (LF 3-5-19) in the region of the nidulus of the abducens, showing evidence of the migration of medullary cells into the anlage of the nerve. The phenomena are similar to those which appear in somewhat advanced stages of histogenesis of spinal somatic motor nerves. As in the latter, the nerve anlage contains both fibrillar and cellular components, the fibrillar portion showing genetic relations with neuroblast cells in the ventro-lateral wall of the neural tube. Evidence that the cellular portion of the nerve is medullary and not mesenchymatous in origin is found in the fact that the cells first appear in the proximal portion of the nerve anlage and that, in successive stages, there appear to be more and more nuclei in this portion of the nerve, and a larger number apparently in the process of migration.

40 A portion of a cross-section (LAD 1-7-17) in the region of the nidulus of the abducens of a 19 mm. embryo, showing the ventral half of the medulla as seen under the low power microscope. The section shows the position of the nidulus of the abducens and its relation to the bundle of deeply stained neuraxon fibers which traverse the marginal zone and enter the nerve root.

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41 A portion of the same section (LAD 1–7–17) enlarged to show the structure of the neuroblasts. These are pear-shaped, deeply stained cells with protoplasm extending into the fibrillar neuraxon process.

42, 43, 44 A series of cross-sections of the anlage of the abducens nerve as seen in a 19 mm. embryo. Figure 42 is the most posterior of the sections. The nerve anlage at this stage consists chiefly of a bundle of deeply stained neuraxons irregularly grouped together among vacuolar spaces and partly enclosed by a layer of mesenchymatous cells. In figure 44, the relations of the neuraxons of the nerve as it subdivides into a branch are shown. The highly refractive granules seen in cross-section correspond with the deeply stained fibers appearing in longitudinal sections.

PLATE 7

EXPLANATION OF FIGURES

Most of the figures are camera drawings with one-twelfth homogeneous oil-immersion objective and No. 6 compensation ocular of Zeiss showing stages in the histogenesis of the trochlearis nerve. Figures 55 and 56 are graphic reconstructions from parasagittal sections as seen under low power objective.

45 and 46 Portions of cross-sections (LAG 1–6–1, 2) of a 19 mm. embryo through the region of constriction between midbrain and hindbrain vesicles, showing portions of the trochlearis anlage as it passes through the mesenchyma lateral to the wall of the brain. The growing tip of the nerve is not shown. At this stage the anlage is wholly fibrillar and its deeply staining fibrils contrast strikingly with the granular vacuolated protoplasm of the surrounding mesenchyma. A thin layer of granular protoplasm may be seen covering portions of the nerve anlage. The fibrils of the nerve may be traced dorsally into the chiasma at the anterior boundary of the cerebellar neuromere, but the nerve has not yet become connected with the myotome of VanWijhe's second somite.

47 and 48 Proximal and distal portions of the trochlearis anlage in cross-sections (MBB 1–4–17 and MBB 1–5–2) of a 21 mm. embryo in the region of the cerebellar neuromere. The nerve anlage differs from the previous stage only in the larger number of fibers composing the nerve bundle. No cells closely associated with the nerve anlage are to be found. The growing tip of the nerve is not shown.

49 A group of neuraxon fibers near the peripheral termination of the trochlearis nerve anlage as seen in a parasagittal section (ME 5–1–4) of a 21 mm. embryo, showing the nerve anlage as a loose brush of neuraxons without any closely associated cells. The highly refractive fibrils show a thin sheath of granular protoplasm.

50 and 51 Portions of the trochlearis nerve anlage as seen in parasagittal sections (MD 2–2–5 and MD 2–2–8) of a 22 mm. embryo, showing the fibrillar character of the nerve. Figure 51 shows a distal and figure 50 a proximal portion of the nerve anlage. In its proximal portion, the trochlearis consists of a compact bundle of neuraxon fibers, naked or with a thin coating of granular protoplasm and devoid of closely associated cells. Distally, however, where the nerve anlage breaks up into a brush of loose fibers, mesenchymatous cells are more closely associated with the individual cells, but there is no evidence of a genetic relation between these cells and the neuraxon fibers.

52 to 56 (See p. 180).

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52 A cross-section of the two roots of the trochlearis anlage near the point of emergence from the neural tube as seen in a parasagittal section (MD 5–1–3) of a 22 mm. embryo. At this stage the nerve anlage consists exclusively of deeply stained neuraxon fibers devoid of nuclei. A sheath of granular protoplasm, however, may be distinguished and mesenchymatous cells show loose relationships with the distal portion of the nerve.

53 One of the roots of the trochlearis as seen in a parasagittal section OA 3–1–8) of a 45 mm. embryo, showing evidence of the migration of nuclei from the neural tube into the roots of the nerve. Proximally the nerve root is cut longitudinally, while distally it is cut transversely. Nuclei appear within the nerve anlage among the neuraxon fibers and also partly within and partly without the neural tube. No mesenchymatous cells are closely associated with the nerve anlage near its point of emergence from the neural tube, and there is no evidence that the nuclei lying within the roots of the nerve have any other than a medullary origin.

54 A portion of a cross-section (MAG 1–6–7) of a 25 mm. embryo in the region of the optic vesicle, showing a peripheral portion of the trochlearis anlage at a stage when it has reached its termination in the superior oblique muscle. The section shows the relation of the trochlearis to the median surface of the muscle and to the ramus ophthalmicus superficialis trigemini which extends along the dorsal surface of the muscle, appearing in cross-section in the figure. Between the two nerve anlagen lies a mass of cells (*gn.sym.*) presumably derived from the r. ophth. sup. trigemini (Miss Platt '91). Both of the distal branches of the trochlearis anlage show a similar aggregation of cells where they cross the ramus ophthalmicus superficialis trigemini. Their derivation and relations show that such groups of cells are to be regarded as sympathetic ganglia and not as primitive sensory ganglia of the trochlearis. They afford as little evidence of the sensory character of the trochlearis as do the sympathetic ganglia associated with somatic motor spinal nerves.

55 A graphic reconstruction of the trochlearis anlage and the structures associated with it made from a series of parasagittal sections (MAA 3, etc.) of a 24 to 25 mm. embryo as seen from the right lateral aspect under low power microscope. At its anterior extremity the ramus ophthalmicus superficialis trigemini terminates in a group of cells derived from the neural crest. The group of cells (*gn.sym.*) associated with the same nerve at the point of crossing of the trochlearis have a similar origin and their relations to the trochlearis anlage are secondary.

56 A graphic reconstruction of the head of a 25 mm. embryo as viewed from the left lateral aspect, based upon parasagittal sections (MAH 3, etc.), showing the relations of the cranial nerves at this stage. In order not to complicate the figure, only two of the eye muscles are shown.

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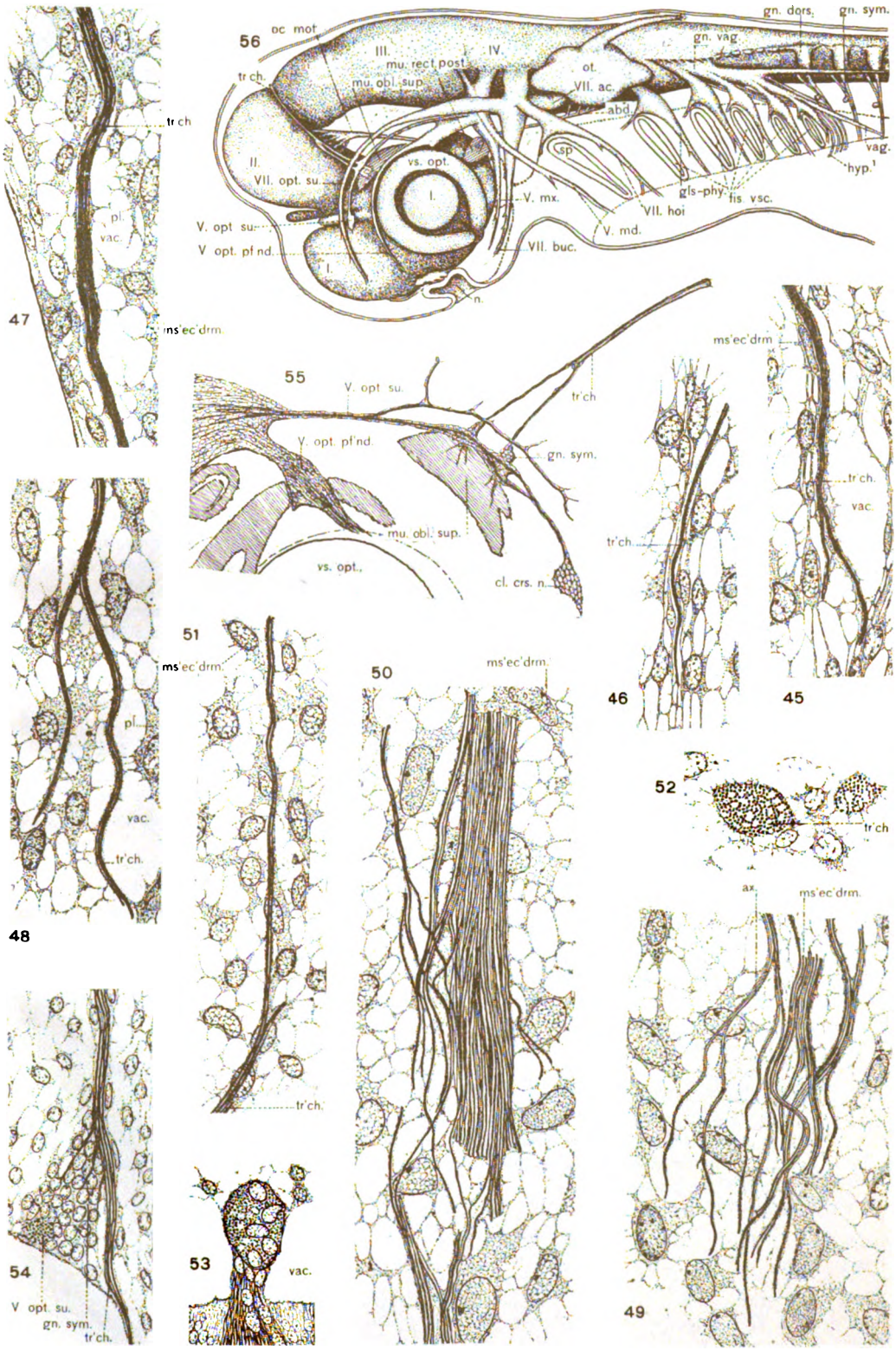

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PLATE 8

EXPLANATION OF FIGURES

A series of camera drawings, showing the histogenesis of the oculomotorius nerve. Most of the drawings were made with one-twelfth homogeneous oil-immersion objective, No. 6 compensation ocular, and Abbe camera.

57 A parasagittal section (KQ 1–4–18) of a 9.5 mm. embryo viewed from the right side, showing the relations of the oculomotorius anlage at the time of its first appearance. The nerve anlage passes directly from the base of the midbrain vesicle towards the first somite of VanWijhe, and closely associated with the pre-cardinal vein.

58 A portion of the same section as in figure 57 (KQ 1–4–18) as seen under a 4 mm. apochromatic objective and No. 6 compensation ocular, showing the oculomotorius anlage as a product of neuroblasts in the base of the midbrain vesicle. Shrinkage has resulted in breaking the roots of the nerve anlage, but there seems no reason to doubt the genetic relation of the nerve anlage with deeply stained neuroblasts lying in the ventral wall of the midbrain, the deeply stained processes of which may be traced to, and beyond the limiting membrane of the brain wall. The nerve anlage shows a deeply stained fibril surrounded by a sheath of granular protoplasm. At the point of union of the two roots of the nerve anlage is a mesenchymatous cell. There is no evidence that this cell has any genetic relation to the nerve anlage, nor is there any evidence of a migration of medullary elements from the neural tube at this stage.

59 A portion of a parasagittal section (KH 2–1–1) of a 9.5 mm. embryo, showing the oculomotorius anlage at a somewhat more advanced stage of histogenesis than that shown in the previous figure, as evinced by the greater number of neuroblasts and neuraxons. There is no evidence of migration of cells from the neural tube at this stage, but several mesenchymatous cells are somewhat closely associated with the nerve anlage. The highly refractive fibrils of the latter are in sharp contrast with the lightly staining vacuolated and granular protoplasm of the mesenchymatous cells.

60. A combination of four sections (KL 2–2–1, 2, 3, 4) of a 10 mm. Squalus embryo in the head region, showing the relations of the oculomotorius anlage, which extends from the midbrain to the first myotome, as seen under the low power microscope.

61 A combination of four sections (KL 2–2–1, 2, 3, 4) showing a part of the oculomotorius anlage in a 10 mm. Squalus embryo. The association of the fibrillar portion of the nerve anlage with medullary neuroblasts in the base of the midbrain is clearly seen. Distally, near the myotome, the nerve breaks up into a brush of separate fibrils, more or less closely associated with mesenchymatous cells. As there is no evidence up to this stage of the migration of medullary cells from the neural tube into the nerve anlage, and as the cells associated with the nerve anlage are more abundant in its peripheral portion near the myotome and the profundus ganglion, the evidence favors the conclusion that these cells are either mesenchymatous or that they are derived from the profundus ganglion, or from both sources.

62 to 71 (See pp. 184 and 185).

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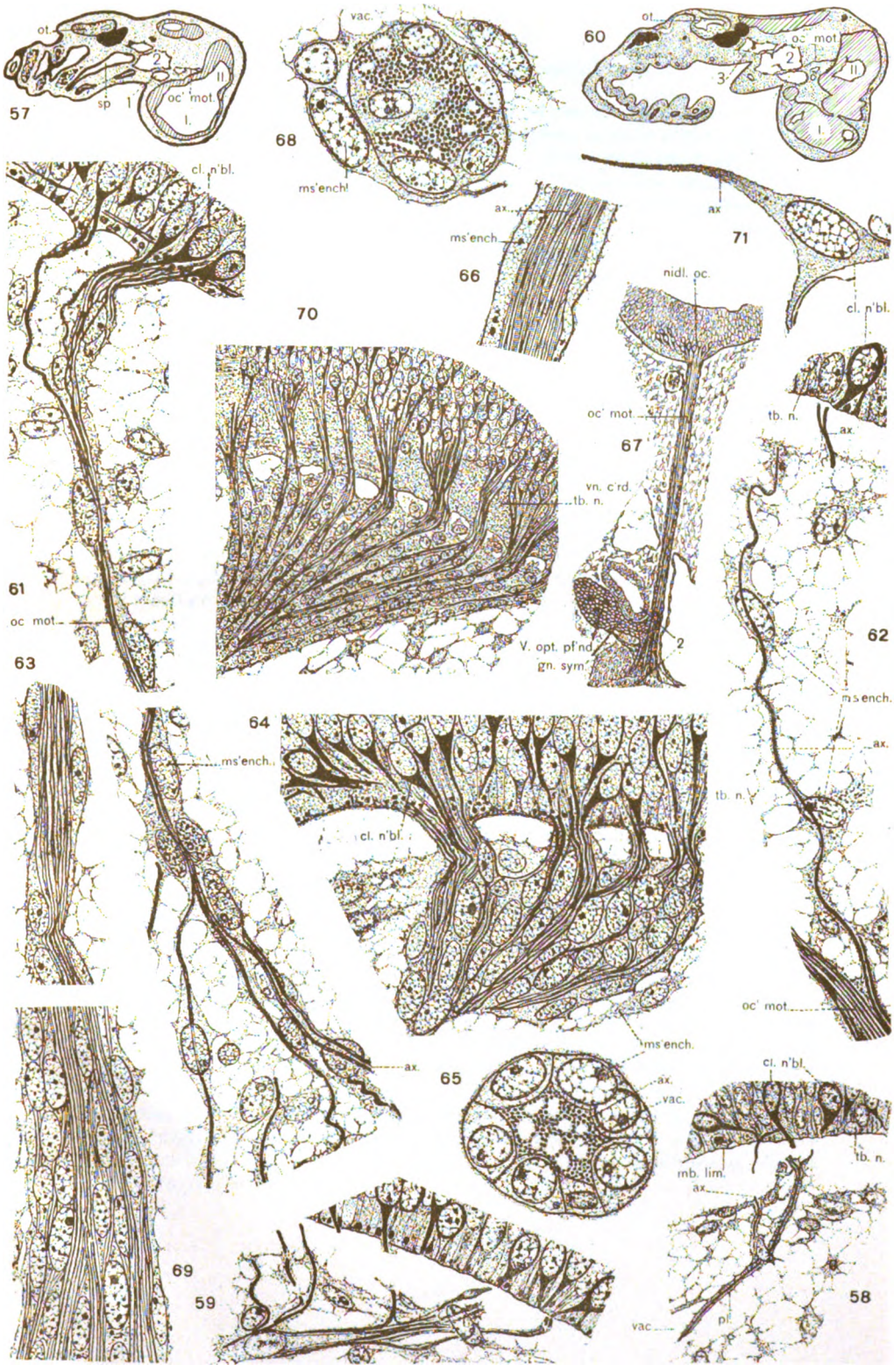

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62 A single neuraxon of the oculomotorius anlage in a parasagittal section (KL 1-5-12) of a 10 mm. embryo, showing its relations with mesenchymatous cells at the base of the midbrain vesicle. The fibril shows the characteristic granular sheath and the evidence which has been interpreted by some investigators in favor of the theory that the neuraxons are differentiated from a protoplasmic reticulum. Such a conclusion, however, ignores the evidence of the peripheral growth of the neuraxons from medullary neuroblasts. The picture is strikingly similar to Gast's ('09) figure 3, plate 13.

63 A portion of the oculomotorius anlage in a parasagittal section (LA 4-2-8) of a 16 mm. embryo, showing the axial fibrillar bundle and the cellular sheath. The conditions are the same as those seen in spinal somatic motor nerves and in the other eye-muscle nerves at similar stages of development. There is no doubt as to the neuroblastic origin of the fibrillar portion of the nerve anlage, but it is not possible to determine positively whether the cellular sheath is ectodermal or mesodermal in origin.

64 A portion of a parasagittal section (LC 2-1-10) of a 16 mm. embryo in the region of the roots of the oculomotorius anlage, showing the relation of fibers of the nerve anlage to neuroblasts lying in the base of the midbrain vesicle. No evidence of cellular migration from the brain into the nerve anlage can be seen, and the source of the cells grouped at the roots of the nerve is doubtful.

65 A cross-section (LG 2-2-9) of the oculomotorius nerve anlage in its peripheral portion in a 15 mm. embryo, showing the bundle of neuraxon fibers with the sheath of mesenchymatous cells. The structure is essentially the same as that in similar sections of the anlagen of spinal ventral nerves. The nerve figured shows approximately two hundred highly refractive granules in the axial bundle, evincing approximately that number of neuraxons in the nerve anlage.

66. A longitudinal section of the oculomotorius anlage in the distal portion of the nerve of a 17 mm. embryo, showing the protoplasmic sheath—no nuclei appear in the portion figured—and the axial bundle of fibers.

67 The oculomotorius anlage as frontal sections (LAG 1-4-24 and 25) of a 16 mm. embryo, showing the relations of the nerve to the ganglion of the ramus ophthalmicus profundus trigemini and to the first somite of VanWijhe. The group of cells lying between the ganglion of the profundus and the oculomotorius may be traced in later stages into the ciliary ganglion of the adult and thus form the anlage of that sympathetic ganglion. The evidence in Squalus seems to favor the view that these cells are derived from the profundus nerve; the possibility, however, that they are in part derived by migration from the brain is not excluded. Of this, however, I am able to find no evidence.

68 A cross-section (LAB 8-13-20) of the oculomotorius anlage in a 17 mm. embryo, showing an early stage in the penetration of the bundle of neuraxon fibers by neurilemma cells. As development continues the number of such cells within the fibrillar bundle steadily increases, beginning at the proximal and distal ends of the nerve anlage.

69 A part of the proximal portion of the oculomotorius anlage in a parasagittal section (MC 4-1-4) of a 21 mm. embryo, showing the penetration of the neuraxon bundle by neurilemma cells.

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70 The nidulus and roots of the oculomotorius anlage in a parasagittal section (ME 3-1-10) of a 21 mm. embryo, showing the increase in the number of roots and the relation of the fibers of the nerve to deeply staining neuroblasts in the ventral wall of the midbrain. With the growth of marginal zone of fibers, the neuroblasts have receded from the limiting membrane of the wall of the midbrain, but they still retain their deeply staining properties and their neuraxon processes may be easily traced through the marginal zone of fibers into the roots of the nerve.

71 A single neuroblast of the nidulus of the oculomotorius in a 46 mm. embryo, showing the beginning of multipolarity and the relation of the neuraxon process.

PLATE 9

EXPLANATION OF FIGURES

A series of diagrams designed to show the metameric relations of the eye muscle nerves and their comparability with spinal somatic motor nerves.

72 A diagram showing the topographic relations of dorsal and sympathetic ganglia to a somatic motor nerve in the trunk region of a Squalus embryo of 15 mm.

73 A diagram showing the relations of the oculomotorius nerve to a sympathetic (ciliary) ganglion and to the ganglion of the ramus ophthalmicus profundus trigemini in a Squalus embryo of 11 mm. A comparison of these relations with those of a spinal somatic motor nerve as shown in figure 72 shows that they are essentially the same. The differences are such as would be brought about, following a reduction of the myotome. The evidence favors the view of the similar mode of formation of the sympathetic ganglion. The reduction of the myotome of VanWijhe's first somite allows the precocious connection of the profundus nerve with the skin and brings about the slightly different topographic relations of nerve, ganglia and myotome shown in the diagram.

74 A diagram showing the relations of the abducens nerve in a Squalus embryo of 13 mm. Like the primitive somatic motor nerves of Amphioxus, the abducens does not become connected with a dorsal nerve and (therefore ?) is not associated with any sympathetic ganglion. Its nidulus, that is, its central relations, and its distribution to somatic musculature, however, sufficiently attest its serial homology with spinal somatic motor nerves. The nidulus of the abducens is elongated, extending through two brain neuromeres (VII and VIII), from both of which the cells which form the vagus ganglion are proliferated.

75 A diagram showing the relations of the trochlearis in a Squalus embryo of 25 mm. Except for the dorsal chiasma, the relations are similar to those of the oculomotorius (fig. 73). The nidulus of the trochlearis lies in the same zone as that of the oculomotorius and immediately behind it in the floor of the cerebellar anlage (third brain neuromere). In precisely the same way that the oculomotorius is associated with the profundus nerve and the ciliary ganglion, the trochlearis is associated with the ramus ophthalmicus superficialis trigemini and with a transient (?) sympathetic ganglion.

76 to 82 (See p. 186).

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76 A diagram showing the greatly modified metameric relations of the eye muscle nerves, based upon the conditions found in Squalus embryos. The diagram is a composite of different stages of development. The relations of the oculomotorius nerve to the ramus ophthalmicus profundus trigemini are those which appear in a 12 mm. embryo, while those of the trochlearis to the ramus superficialis are such as appear in a 25 mm. embryo. The ramus recurrens of the abducens appears in a 19 mm. embryo. The neuromeres and somites are as they appear in much earlier stages of development. The diagram is not intended to show any hypothetical stage in the phylogeny of vertebrates, but merely to present graphically the highly modified metameric relations of the eye muscle nerves to the primary neuromeres and the somites of VanWijhe.

77 A diagram of the left lateral aspect of the head of a Petromyzon embryo of 50 mm., showing the relations of the post-otic myotomes and their associated ventral nerves. The innervation of the first three post-otic myotomes (4, 5, 6) by the ventral nerves of the ventral nerves of the fourth and fifth post-otic myotomes (7, 8) is especially to be noted, as is, also, the splitting of the first post-otic myotome (4) along the dorso-lateral line into a dorsal and ventral division. The homology of the first post-otic somite of Petromyzon with the fourth somite of Squalus is based on the evidence given by Koltzoff ('02).

78 A diagram based upon a reconstruction of a 3.5 mm. embryo of Petromyzon by Koltzoff ('02) showing the splitting of the anterior post-otic myotomes into median and lateral divisions. In order to explain the present relations of the eye-muscle nerves (fig. 76) to the pre-otic myotomes in Squalus, a similar subdivision of the myotomes of VanWijhe's first, second and third somites may be assumed.

79 A diagram based upon a cross-section of a Petromyzon embryo of 3.5 mm., showing the three divisions (my. 4 m., my. 4 d. l., my. 4v. l.) of the first post-otic myotome, and their relations to the otic capsule. The hypothetical primitive connection of a somatic motor nerve with the median (transient) division of the myotome is shown. The two divisions of the myotome lateral to the otic capsule are permanent and become innervated by the ventral nerves of the fourth and fifth post-otic myotomes. By a similar substitution, it may be inferred, the rectus posterior muscle—a pre-otic muscle—has become innervated by the abducens—a post-otic nerve.

80 A diagram based upon a frontal section in the occipital region of a Petromyzon embryo of 4 mm., showing the relations of the anterior most post-otic ventral nerves to the myotomes. The division of these myotomes into a median portion and a portion lateral to the otic capsule is shown.

81 A diagram of the left lateral aspect of a Squalus embryo, showing the hypothetical primitive relations of the eye muscles to the lateral trunk musculature. Those myotomic divisions which are not functional in the adult Squalus are indicated by broken lines. Only those pre-otic myotomes which have acquired connection with the bulbus oculi and have become functional as eye muscles have persisted. The homologues of myotomes 4, 5 and 6, however, are functional in Amphioxus and Petromyzonts.

82 A diagram intended to show the conditions under which the dorsal chiasma of the trochlearis has been acquired. The left side of the diagram shows an hypothetical stage when the myotome of VanWijhe's second somite was split into three moieties. The right side of the diagram corresponds in all essential respects with the conditions found in a 25 mm. Squalus embryo. For an interpretation of the figure, see p. 114 of the text.

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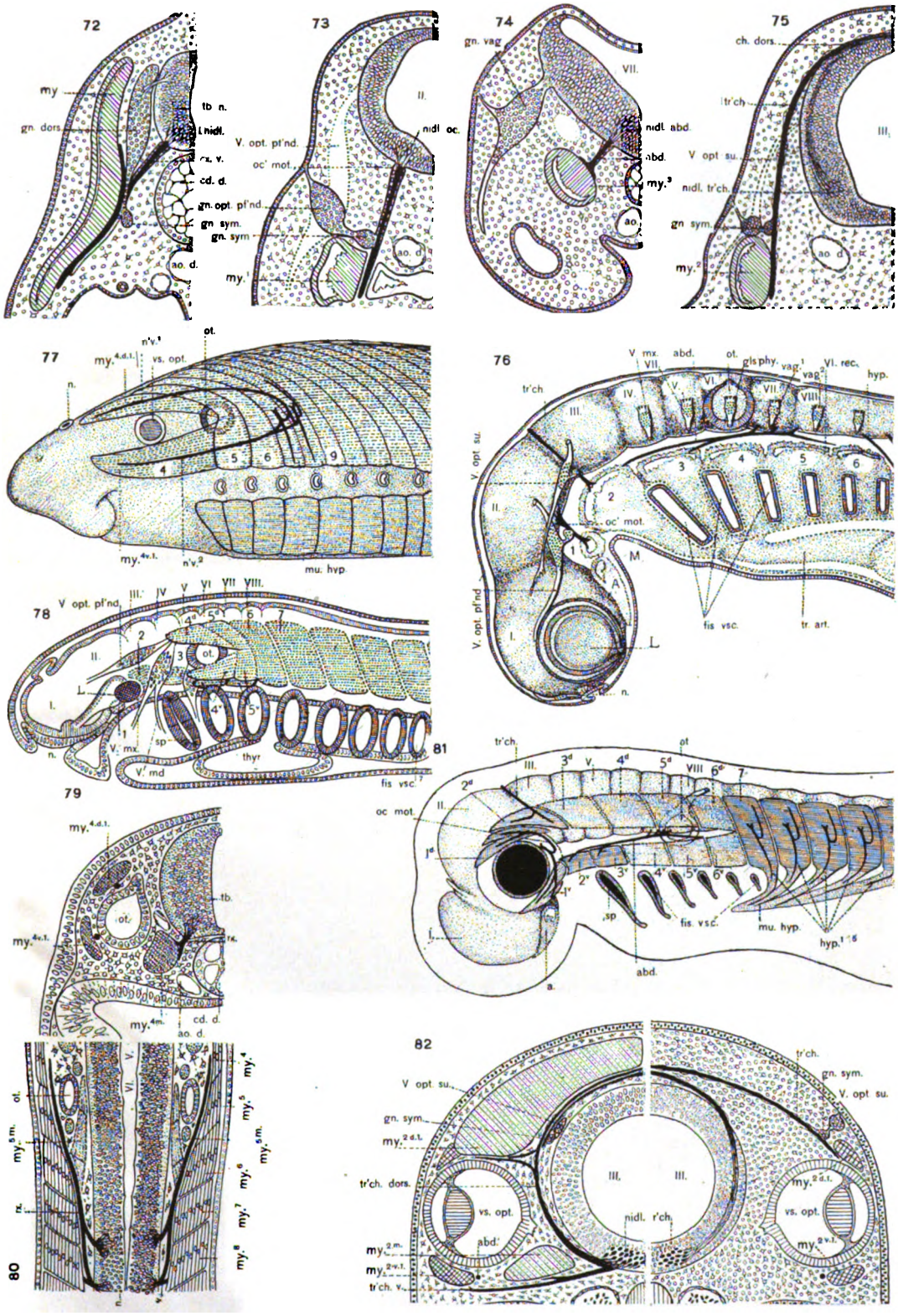

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